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VARIATION IN VESSEL LENGTH WITHIN ONE GROWTH RING OF CERTAIN ARBORESCENT DICOTYLEDONS

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Bisset *et al.* (1950 *a*, *b*) have recently demonstrated that the length of the imperforate tracheary cells within the limits of one growth ring is subject to significant variability under certain conditions of growth of the secondary xylem. They have shown that in gymnospermous and dicotyledonous woods characterized by the presence of distinct growth rings, the fibres generally undergo a progressive increase in length from the first-formed early wood to the last-formed late wood; on the other hand, in those secondary xyla where the formation of distinct growth rings is absent, the fibres fail to exhibit any significant kind of mode even when considerable quantum of wood representing the growth of several years is analysed.

In hard woods with storeyed cambia and distinct growth rings, Chalk *et al.* (1955) observed that the length of the fibres rose to a maximum in the middle of the ring and dropped abruptly on the ring boundary; the length of the parenchyma strands, on the contrary, remained constant throughout the ring. The other cell type of the secondary xylem that has not been studied from the point of view of size variability within one growth ring is the vessel. The present contribution deals with the results obtained in course of exploratory investigations on the range of size variations of vessel members within a growth ring.

Investigations along these lines on vessels present certain difficulties as a result of which the choice of species becomes limited. Woods with very wide vessels and those with sparse pore distribution cannot possibly yield the adequate number of observations needed in connection with studies involving reasonably accurate average values. Thus, the selection of material of woods with definite growth ring becomes further confined to those with relatively smaller-lumened vessels and denser pore distribution. Data have been obtained from the following species:—

A. Woods showing definite growth rings

1. Ring porous (including graded arrangement)
   Acanthopanax ricinifolia Sieb. and Zucc.
   Alangium chinense (Loureiro) Harms
   Cipadessa baccifera Miq. (vessels and rays storeyed)
   Gilibertia trifida Makino
   Sassafras officinale Nees. and Eberm.
   Tectona grandis L.

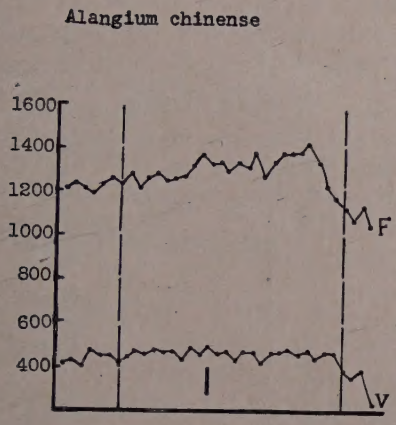
2. Diffuse porous
   Alangium kurzii Craib
   Alangium rotundifolium (Hasskarl) Bloemb.
   Platanus occidentalis Hook. and Arn.

B. Woods without definite growth rings
   Alangium javanicum (Bl.) Wangerin
   Alangium salvifolium (Linn. f.) Wangerin
   Pancheria ternata Brongn. and Gris.

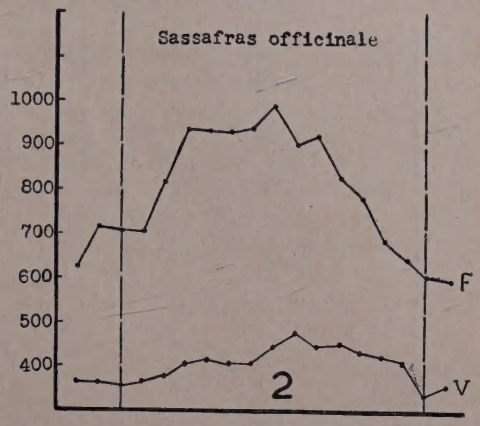
The techniques employed for the preparation of materials were in essential similar to those adopted by Bisset *et al.* (1950 *b*). In all cases, fairly mature and more or less comparable specimens were utilized, taking particular care to avoid structural defects. In the case of woods with relatively narrow-lumened vessels, serial tangential sections varying in thickness between 80 and 120 μ were taken, while for woods with much larger diameters the thickness was adjusted between 100 and 200 μ. The sections were macerated in Jeffrey's reagent at 60° C. Optimum maceration was obtained at the end of three to four hours. The macerated tissues were squashed by gentle shaking in water in a glass tube. The suspension thus obtained was transferred on to slides with the help of a medicine dropper. One hundred vessel members and the same number of fibres were measured for length values from each tangential section; vessel diameter, wherever taken, has been measured from the corresponding vessel member which was utilized for obtaining the linear dimension. All measurements were taken directly under the microscope with calibrated lens combination. In the graphs reproduced as text-figures the average length values for fibres at corresponding distances as of the vessels are also given for comparison.

Results and Discussion

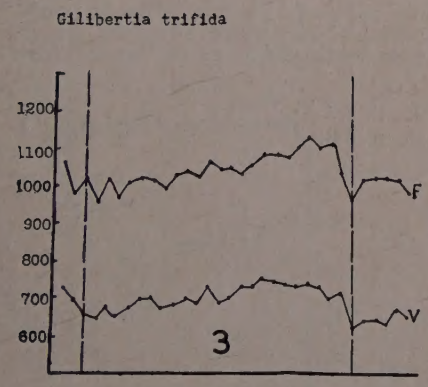
In ring porous woods the average vessel length in the later-formed region of a growth ring is always greater than that in the earlier-formed part (Text-Figs. 1–5). This trend is in accordance with that obtained for the fibres of the corresponding species as also for the fibres of other species by Bisset *et al.* (1950 *b*). In most instances the peak for vessel length lies somewhere in the later-formed region of the growth ring. In *Cipadessa baccifera* (Text-Fig. 6) the vessel members retain more



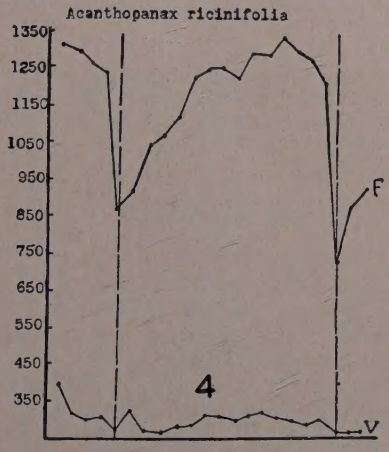
TEXT-FIG. 1



TEXT-FIG. 2



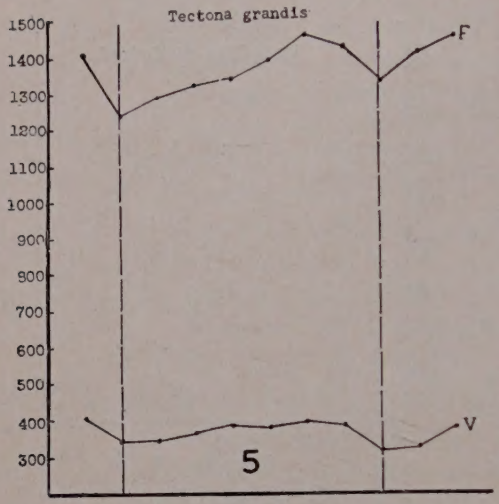
TEXT-FIG. 3



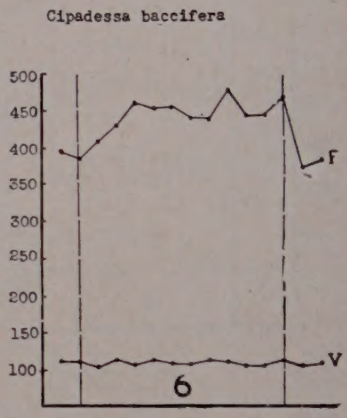
TEXT-FIG. 4

or less the same length values throughout the growth ring, although the curve for the fibres exhibits a trend similar to that shown by many other woods with distinct growth rings. This situation appears to be just what is to be expected in view of the storeyed nature of the cambium, wherein the feature is particularly well established in relation to the vessel member. Incidentally, it may also be noted that in woods with storeyed cambia the length of the vessel remains relatively constant from the earlier-formed to the later-formed secondary wood along the entire diameter of the stem (Bailey and Tupper, 1919) and recently a parallel trend has been established for storeyed wood parenchyma strands also (Chalk *et al.*, 1955).

In *Alangium chinense* (Text-Fig. 1) the attainment of maximum length of vessel members appears to become established at the beginning

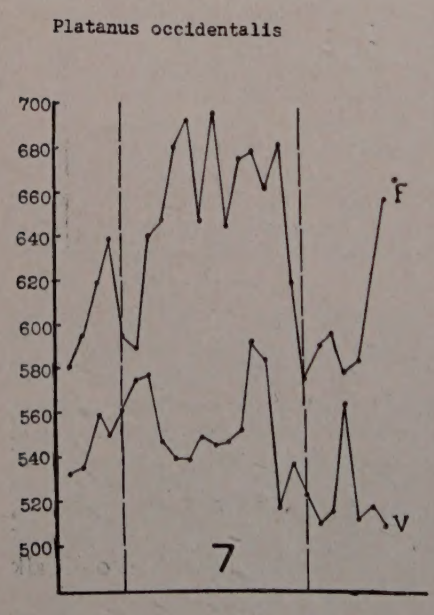


TEXT-FIG. 5

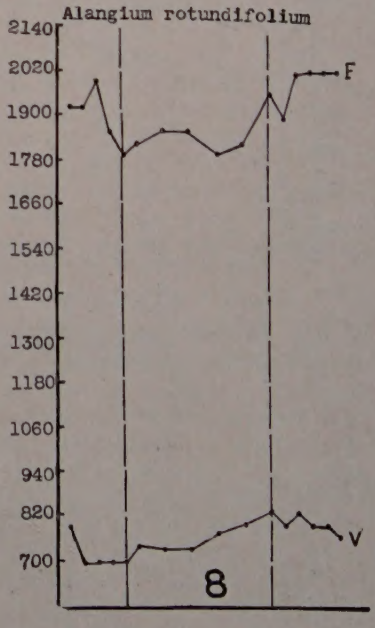


TEXT-FIG. 6

TEXT-FIGS. 1–6. Length-on-age curves for fibres and vessel members in woods. with distinct growth rings (F and V respectively). The numbers along the vertical axis are in microns. Limits of growth rings are represented in vertical broken lines. Ring porous woods.

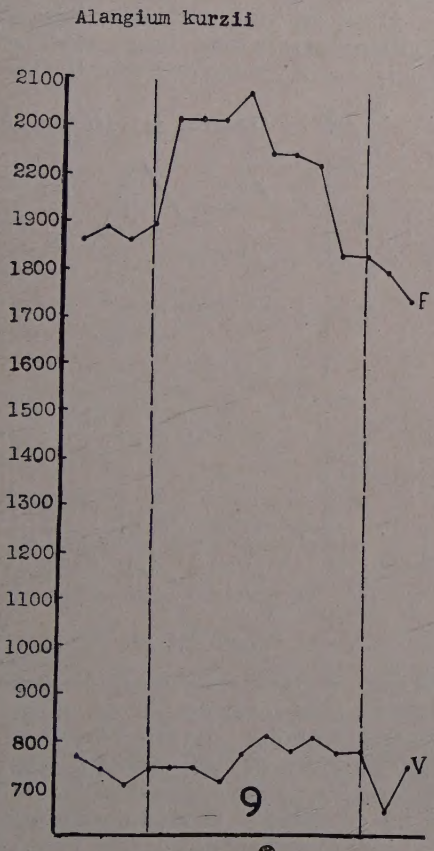


TEXT-FIG. 7

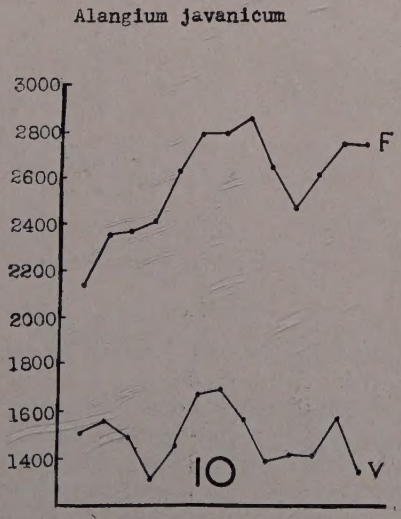


TEXT-FIG. 8

of the growth period itself and this acquired length remains relatively constant at successive distances within the ring, finally dropping down abruptly at the junction region of the next growth ring as in other ring porous species. In woods which possess distinct growth rings and diffuse pattern of distribution of pores, the mode shown by the average length of vessel member parallels the one described for ring porous woods (Text-Figs. 7–9). In contrast to these two categories of woods in which the growth increments are clearly defined, woods in which growth rings are



TEXT-FIG. 9



TEXT-FIG. 10

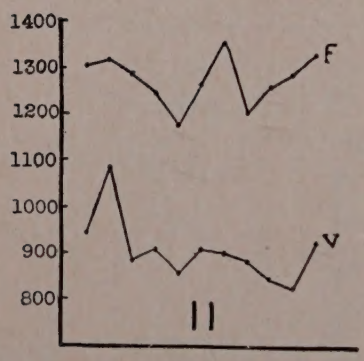
TEXT-FIGS. 7–10. Figs. 7–9. Length-on-age curves for fibres and vessel members in woods with distinct growth rings (F and V respectively). Diffuse porous woods. Fig. 10. Length-on-age curves for fibres and vessel members in woods without growth rings. Rest of the legend as in previous figures.

absent fail to exhibit specific curves in regard to the vessel length over stretches of xylem tissue formed during several years (Text-Figs. 10–12)

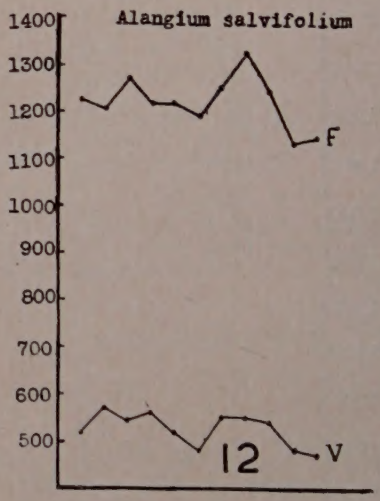
On the whole, it may be observed that although the trends shown both by fibres and vessels within a growth ring conform to the same basic

kind the degree of expression of the feature is much more pronounced in the case of fibres than in vessel members of the same secondary xylem of any species. This difference is possibly a reflection of the inherent tendency of the fibre initial cell to undergo extensive apical elongation during maturation while such a feature is comparatively minimised in the ontogeny of a vessel member.

The trend shown by the vessel members and fibres, both in the diffuse porous and ring porous woods, as stated already, indicates a gradual increase from the beginning of the growth ring. In so far as the fibre length variation within a ring is concerned, it has been shown by Chalk *et al.* (1955) that shorter length at the beginning of a growth ring

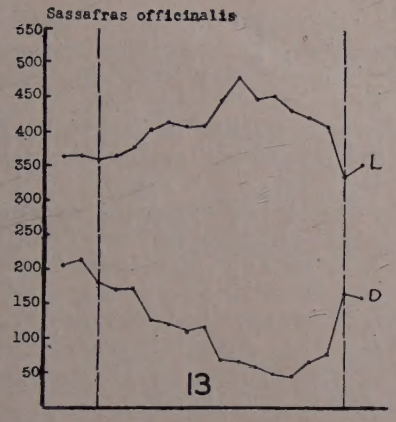


TEXT-FIG. 11

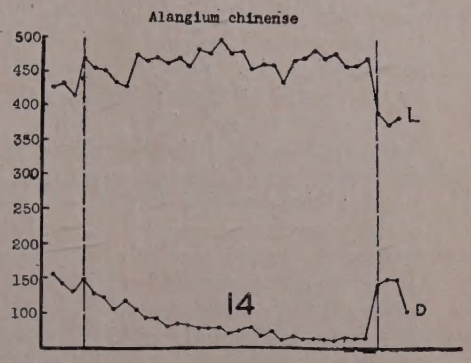


TEXT-FIG. 12

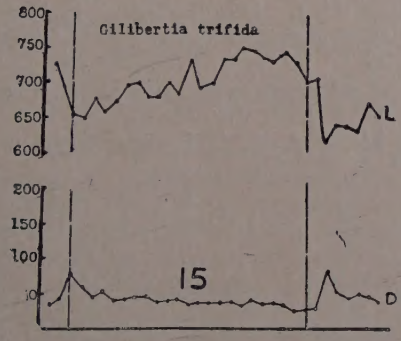
is correlated with a relatively rapid rate of pseudotransverse divisions of the fusiform initials, thereby inhibiting to some extent the phenomenon of apical elongation of the concerned fibres; on the other hand, towards the later-formed region, the frequency of such divisions slows down so that the derivative imperforate tracheary cells possess the required time to undergo maximum readjustment in terms of vertical elongation. This postulation appears to afford a logical explanation in the case of vessels of diffuse porous and ring porous woods as well. Although this factor may be operative in the case of vessels of ring porous woods, it is likely that the vessel diameter also could be a factor involved in the phenomenon. In typical cases of graded porous woods, the diameter of the vessel members is negatively correlated with their corresponding length within a growth ring (Text-Figs. 13–16); the *r*-values for the species investigated are of the order of −·92 for *Sassafras officinale* and *Acanthopanax ricinifolia*, −·69 for *Alangium chinense* and −·68 for *Gilibertia trifida*. From these data one is led to assume that the degree of lateral expansion of the vessel member may be regarded as an additional factor



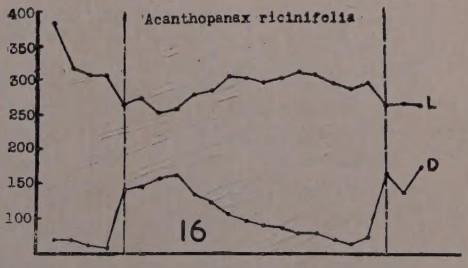
TEXT-FIG. 13



TEXT-FIG. 14



TEXT-FIG. 15



TEXT-FIG. 16

TEXT-FIGS. 11–16. Figs. 11–12. Length-on-age curves for fibres and vessel members in woods without growth rings. Rest of the legend as in previous figures. Figs. 13–16. Relationship between length and diameter of vessel members in graded porous woods (L = length, D = diameter).

influencing the formation of shorter vessel members at the beginning of the growth ring, at least in so far as the graded porous woods are concerned.

The results of this study raise an important consideration. Are the fluctuations seen in vessel length within one growth ring due to corresponding changes in the fusiform initials of the cambium that develop into vessels, or due to subsequent apical elongation of the vessel members during maturation ? It is proposed to discuss these and allied questions in a later contribution.

Summary

Size variations of vessel members within a growth ring of certain arborescent dicotyledonous woods have been studied. The average vessel length gradually increases from the earlier-formed to the later-formed part of the growth ring with the peak value lying towards the later half of the ring. This trend is similar in quality to that exhibited by the length of fibres; however, it is less pronounced quantitatively in the case of vessels. The rapidity of pseudotransverse divisions in the fusiform initials at the beginning of the growth ring appears to explain the formation of shorter vessel members both in diffuse and ring porous woods; the retarded rate of cell division toward the later-formed part of the growth ring appears to result in the differentiation of longer vessel members. In the case of certain ring porous woods, the vessel diameter is negatively correlated with its length within a growth ring. This behaviour also is suggested as a factor of some significance in controlling the vessel length within a growth ring of such woods.

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THE EMBRYOLOGY OF *GALIUM ASPERIFOLIUM* WALL.

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Introduction

The life-history of *Galium asperifolium* Wall. (= *Galium mollugo* Linn. has been worked out by Lloyd (1902) and Fagerlind (1937). Certain important aspects of the life-history have been left out by these authors. A brief account of my observations is given here.

The material was collected by Dr. Reayat Khan and Mr. Akhtar Hasan from Mussoorie and very kindly handed over to me. F.A.A. was used as fixative. Dehydration was done in alcohol-xylol series and embedding in paraffin wax. Sections were taken at 7–10 microns. Staining was done in safranin and fast green.

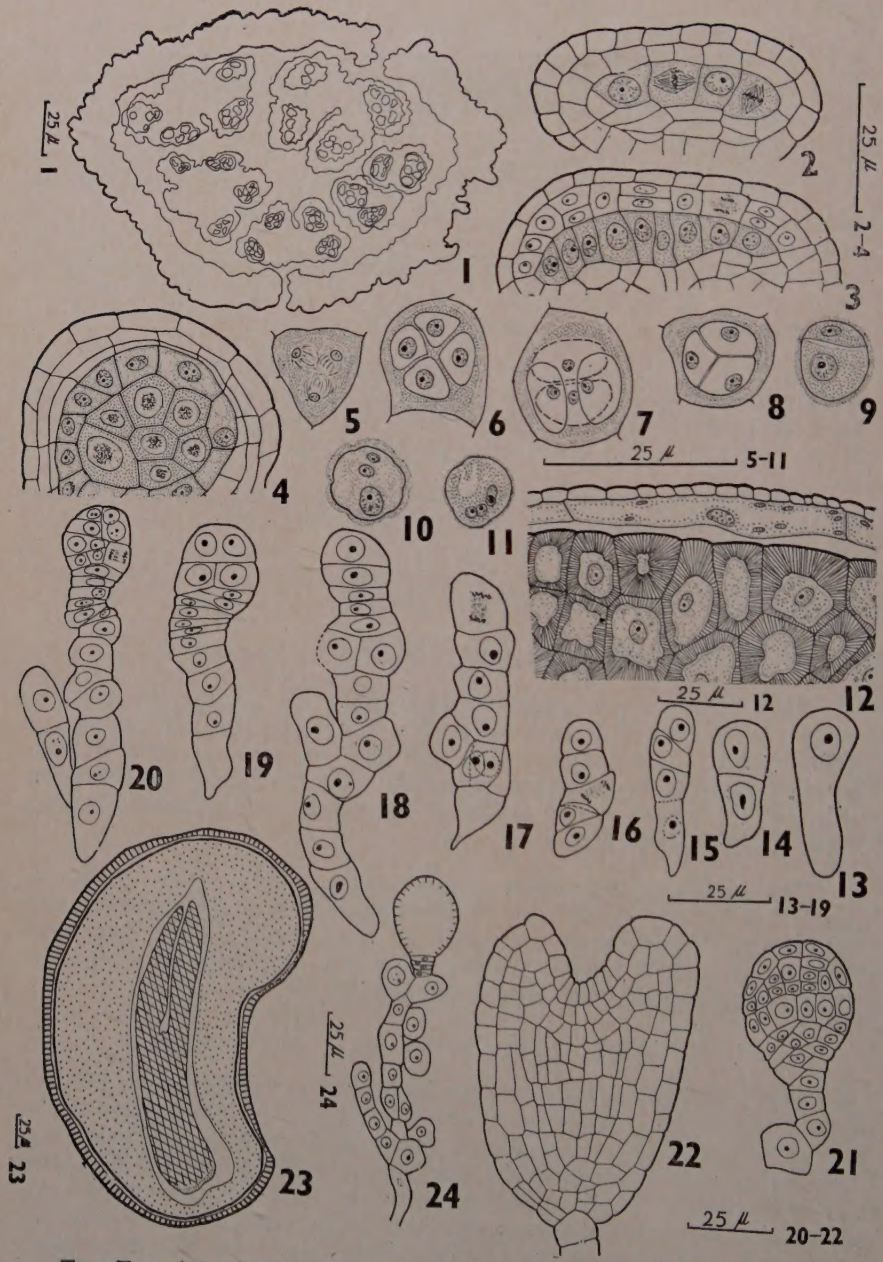
Megasporangium and Female Gametophyte

The ovules are unitegmic and tenuinucellate. The nucellus is represented by a few epidermal cells. An integumentary tapetum is not differentiated. It is interesting to note that the presence of an integumentary tapetum has not been recorded in any member of the Rubiaceæ although the ovules in this family are unitegmic and tenuinucellate like most of the Tubifloræ.

The female archesporium is multicellular. Embryo-sac is monosporic and 8-nucleate with the usual organization of egg apparatus and antipodals. The lowest antipodal is abnormally long. Sometimes twin sacs may be formed. These findings are in accordance with those recorded by Lloyd (1902) and Fagerlind (1937).

Microsporangium and Male Gametophyte

There are usually four stamens (and four petals) but in one case five stamens (and five petals) were seen (Text-Fig. 1). The larger corolla segment in Text-Fig. 1 represents three petals and the smaller two. The anther wall develops in the usual manner (Fagerlind, 1937). After the differentiation of the sporogenous tissue and the primary wall layer, the cells of the former undergo divisions to produce some seven rows of cells, each row about nine cells long (Text-Figs. 2–4). The microspore mother cells divide simultaneously. Cytokinesis takes place by centripetally advancing constriction furrows (Text-Fig. 5). The microspore



TEXT-FIGS. 1–24. *Galium asperifolium* Wall. Fig. 1. T.S. of flower having 5 stamens. Fig. 2. L.S. of anther showing mitotic division of sporogenous cells. Figs. 3 and 4. Stages of wall development of anther. Fig. 5. Cytokinesis in

tetrad formation. Figs. 6–8. Isobilateral, decussate and tetrahedral arrangement of microspore tetrad. Fig. 9. Two-nucleate pollen. Fig. 10. Three-nucleate pollen. Fig. 11. Pollen with four nuclei. Fig. 12. A section of mature seed showing the integumental epidermis, the hypodermal layer and thick-walled endosperm cells. Fig. 13. Zygote. Fig. 14. Two-celled proembryo formed by transverse division of zygote. Fig. 15. Linear proembryonic tetrad. Fig. 16. Five-celled proembryo, one of the cells is undergoing longitudinal division. Figs. 17–23. Stages in the formation of suspensor and the embryo. Fig. 24. Embryo showing the uniseriate filamentous structure of a branched suspensor. One of the cells of the suspensor has divided longitudinally.

tetrads may be isobilateral, decussate or tetrahedral (Text-Figs. 6–8). At the shedding stage the microspores possess three nuclei (Text-Figs. 9 and 10). The pollen is spherical. At the equator there are 6 or 7 bulges. One pollen grain possessed four nuclei almost of equal size and these were aggregated on one side of the pollen (Text-Fig. 11).

Endosperm

The endosperm is of nuclear type. The walls are laid down when 8–16 endosperm nuclei have been formed. The cells thus formed contain very dense cytoplasm. In older stages cytoplasm becomes less dense and the cells contain a large amount of starch grains.

In older stages of the fertilized embryo-sac the cells of the integument surrounding the embryo-sac of *G. asperifolium* increase in size, become vacuolated and then gradually begin to disorganize. The process of disorganization of the integumental cells continues till only one layer of cells below the epidermis is left. This hypodermal layer has tangentially elongated and highly vacuolated cells which contain plastids (Text-Fig. 12). Thickening material begins to accumulate in the outermost layer of the endosperm cells. Gradually the process extends to the inner cells also. As the accumulation of thickening material in the cells increases there is decrease in the starch content and the protoplasm is very much reduced in amount (Text-Fig. 12). At maturity 5–7 layers of the endosperm cells surround the embryo.

Embryo

The zygote divides transversely (Text-Figs. 13 and 14). The proembryonic tetrad is linear (Text-Fig. 15). The exact sequence of cell divisions leading to the formation of the suspensor and the quadrant stage of the embryo could not be followed. However, on the basis of available stages of embryo development, it may be assumed that probably the main body of the embryo is formed out of the cells produced by the divisions of the apical cell (Text-Figs. 16–23). It is noteworthy that sometimes the suspensor cells undergo longitudinal division (Text-Figs. 16, 17, 20 and 24). The suspensor haustoria are prominent. Individual cells of the suspensor bulge out between the cells of the endosperm. Sometimes these haustorial cells undergo transverse divisions and form uniseriate filamentous structures (Text-Figs. 20 and 24). They do not seem to cause any visible damage to the endosperm cells. They remain intact up to quite late stages of embryo development. Thus the embryo-

geny of *G. asperifolium* conforms to the Sherardia variation of Solanad type (Johansen, 1950).

Discussion

Tetramerous flowers are common in the Galieæ. The occasional occurrence of 5 stamens and 5 petals in the flower of *G. asperifolium* may be interpreted as suggesting that the tetramerous condition in *Galium* might have been reached by reduction of a pentamerous flower.

The mature microspores of *G. asperifolium* possess three nuclei as in other members of the family which have been studied in this respect.

All the Rubiaceæ have nuclear endosperm except *Ophiorrhiza mungos* (Ganapaty, 1956). In all the Galieæ so far studied and in *Putoria* (Fagerlind, 1936) the endosperm begins to develop in the form of a layer enclosing a central cavity. The walls are laid down in the peripheral protoplasmic layer and then the cellular endosperm gradually fills the whole embryo-sac cavity.

The seed coat in *G. asperifolium* consists of two layers of cells. A two-layered testa has also been reported in *Oldenlandia alata*, *Dentella repens* (Raghavan and Rangaswamy, 1941) and *Vaillantia hispida* (Lloyd, 1902). On the other hand in *Oldenlandia corymbosa* and *Borreria hispida* (Farooq, 1952, 1953), *Callipeltis cucullaria* and *Sherardia arvensis* (Lloyd, 1902) the testa is one-layered.

The embryogeny in the Rubiaceæ follows the Solanad type. Sherardia variation is usually present in the Galieæ. The suspensor is uniseriate and haustorial. Lloyd (1902) has recorded longitudinal divisions of the suspensor cells in *Vaillantia* and Souèges (1924, 1925) in *Sherardia arvensis*. Fagerlind (1937) failed to find such divisions of suspensor cells among plants he studied. In *G. asperifolium* the suspensor cells occasionally undergo longitudinal division and the haustorial cells which protrude into the endosperm may undergo transverse division and form filamentous structures.

Prominently developed suspensor haustorial cells have been recorded in many Rubiaceæ, *e.g.*, *Crucianella ægyptica*, *Rubia tinctoria* and *Asperula setosa* (*see* Johansen, 1950) but the development of branched suspensor is found only in *Galium asperifolium*. These branches of the suspensor could also be interpreted as leading to cleavage polyembryony provided their development into embryos could be definitely established.

Summary

1. The nucellar epidermis and the female archesporium are multicellular. The megaspores germinate by tube formation. Almost the entire embryo-sac is organized in the micropylar canal. It is monosporic and 8-nucleate.

2. Sometimes five stamens and five petals may develop instead of four. The microspore tetrads are tetrahedral, decussate or isobilateral. The pollen is 3-nucleate at the shedding stage.

3. The endosperm is nuclear and the testa is two-layered.

4. The embryogeny follows the Sherardia variation of Solanad type. The suspensor is long and haustorial in nature. It is uniseriate but some of its cells may undergo longitudinal division. The haustorial cells of the suspensor may also undergo transverse division and form filamentous structure.

I am greatly indebted to Dr. Reayat Khan for his help in writing this account

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MORPHOLOGY AND EMBRYOLOGY OF *CARDIOSPERMUM HALICACABUM* LINN.

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Introduction

Members of Sapindaceæ have attracted attention of botanists for a variety of reasons. The anomalous structures in the stem in many genera were of special interest.

Anatomical investigations on the vegetative organs of the family have been summarised by Metcalfe and Chalk (1950) in which reference is also made to *Cardiospermum*. Saunders (1939) has briefly described the floral anatomy of *Cardiospermum*. According to her the gynœcium consists of three fertile and three sterile carpels. Khan (1929) studied the pollination and fruit formation in *Litchi*. Schnarf (1931) has reviewed the early literature on the embryology of the family. Mauritzon (1936) gave a short account of the embryology of some members of Sapindaceæ including *Cardiospermum*. Joshi (1938) observed parthenocarpy in *Dodonea viscosa*. David's (1938) account of the embryology of the Sapindaceae in which *Cardiospermum* has also been mentioned does not give many details. Banerji and Chaudhuri (1944) described the development of gametophytes in *Litchi chinensis*. Kadry's (1946, 1950) observations on the embryology of *C. halicacabum* differ, in some respects, from those of Mauritzon and ours. The present work was therefore undertaken to describe in detail the anatomy of the node and petiole, morphology of the inflorescence and flower, and the embryology of *C. halicacabum*. This plant is widely used in indigenous medicine for a variety of diseases and as an antidote for snake bite and scorpion sting (Kirtikar and Basu, 1933).

Material and Methods

The plants flower on the onset of Monsoon and the seeds are shed towards the end of December. Materials were collected from Changanacherry, Chengannoor, and Moovattupuzha (Kerala State) in June 1957 and from Khetri (Rajasthan), and Botanical Garden, Birla College, Pilani, during August to November 1957. They were fixed in formalin-acetic-alcohol and Carnoy's fluid. The usual methods of dehydration

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and embedding were followed. Sections cut at 6–16μ were stained in safranin and fast green, and Heidenhain's iron hæmatoxylin counterstained with fast green. Some slides were also stained with erythrosin and crystal violet and these were particularly useful for studies on floral anatomy. Whole mounts of pollen grains were made according to the methyl green glycerine jelly method (Wodehouse, 1934) with the difference that methyl green was replaced by methyl blue.

Anatomy of Node and Petiole

The alternate and biternate leaves have nine serrate leaflets. The slightly sheathing petiolar base has two tiny-free lateral stipules. The petiole is traversed by eight vascular bundles of which four are conspicuously larger than the rest.

The young stem shows the primary structure and early phase of secondary growth. A transverse section just below the node shows the foliar supply of three strands, of which the central is more prominent than the other two; each strand causes a gap in the stele. The lateral strands after giving a branch each to the stipule fuse with the median in the subnodal region to divide again into eight before entering the petiole. Text-Figure 1 shows the details of petiolar supply.

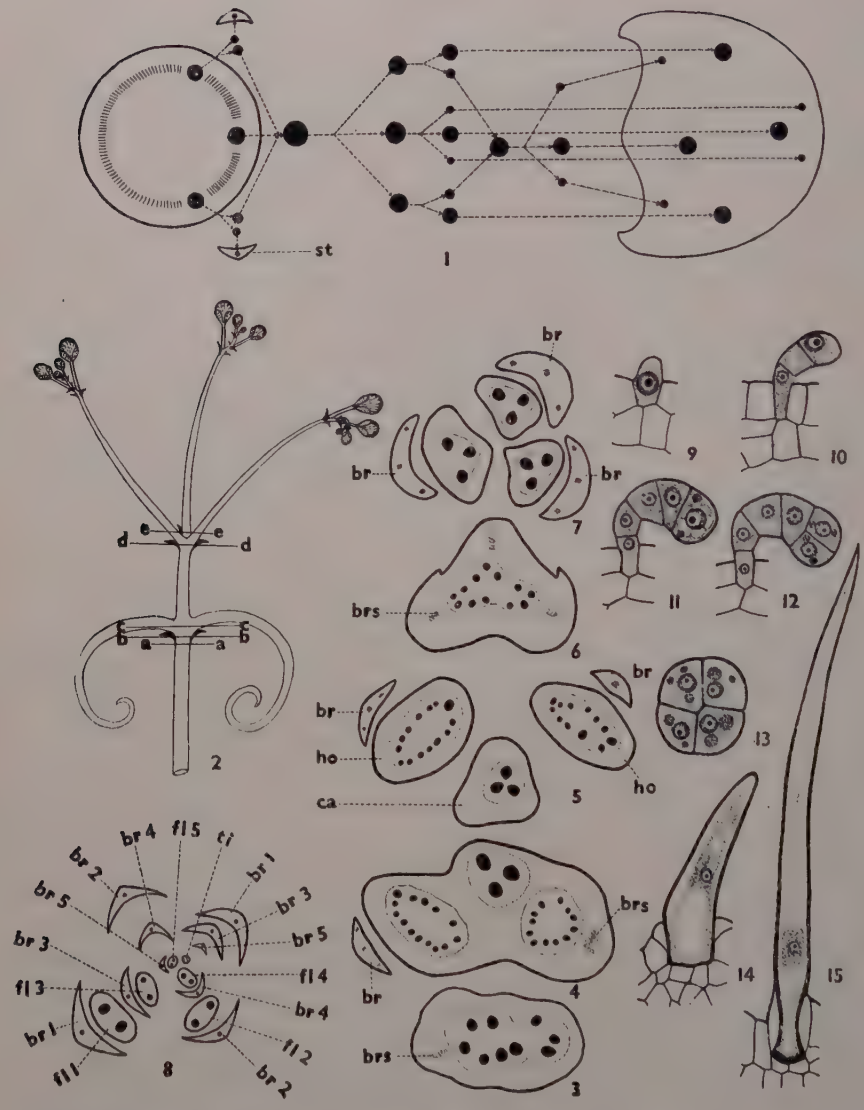
Inflorescence

The inflorescence axis bears two cirrhose tendrils (Text-Fig. 2) which aid in climbing. Each tendril is subtended by a bract. The peduncle divides at its tip into three branches subtended by bracts. Each branch towards its apex bears four or five pairs of decussate bracts. The bracteate flowers are arranged in two rows on one side of the axis, *i.e.*, at 90 degrees, the alternating ones being in a line. They open acropetally. Sometimes undeveloped primordia may be seen in the axils of sterile bracts. The tips of the branches do not terminate in flowers. Text-Figure 8 shows the face view of one of the branches.

The peduncle has four bundles in the basal region which divide to form nine to ten bundles. Below the tendrils the stele becomes three-lobed and from the lateral lobes a trace diverges out to each bract (Text-Fig. 3). At a higher region the bract shows three bundles (Text-Fig. 4). Close above, the stele breaks up into three, each consisting of three bundles and surrounded by a sclerenchymatous sheath. The lateral groups divide to form a large number of bundles and supply the tendrils (Text-Figs. 4, 5). The central stele of three bundles enters the main axis of the inflorescence and divides into three groups of three bundles each after supplying a trace to every bract that subtends the branches of the inflorescence. Each branch receives three bundles which divide into a large number of bundles and supply a trace to each bract and two traces to the pedicel of every flower. After the uppermost flower has been supplied the residual stele fades away at the tip.

External Morphology of the Flower

The polygamous flowers are tetramerous and zygomorphic. The outer two sepals are smaller than the inner. The petals are united in



TEXT-FIGS. 1–15. Fig. 1. Schematic representation of vascular anatomy of node and petiole. Fig. 2. Inflorescence, ×2·5. Figs. 3–7. Inflorescence axis cut at levels marked *aa*, *bb*, *cc*, *dd*, and *ee* marked in Fig. 2 ×25. Fig. 8. Schematic representation of flowers viewed from above. Figs. 9–12. Development of multicellular gland, × 500. Fig. 13. T.S. Multicellular gland, × 500. Figs. 14–15. Young and old unicellular hair from ovary wall, ×500. (*br*, bract; *brs*, bract supply; *ca*, central axis of the inflorescence; *fl*, pedicel of flower; *ho*, tendril; *st*, stipule; *ti*, tip of the inflorescence.)

TEXT-FIGS. 16–39

TEXT-FIGS. 16–39. Figs. 16–28. Serial transections from pedicel upwards of male flower, ×30. Figs. 29–39. Serial transections from the base of the gynœcium upwards of a female flower, ×15. (*at*, staminal trace; *cd*, dorsal trace; *cr*, carpellode; *csp*, common trace for the small sepal and petals; *di*, disc; *ds*, disc supply; *ot*, ovular trace; *pe*, petal; *pt*, petal trace; *sc*, scale of the petal; *sm*, secondary marginal.)

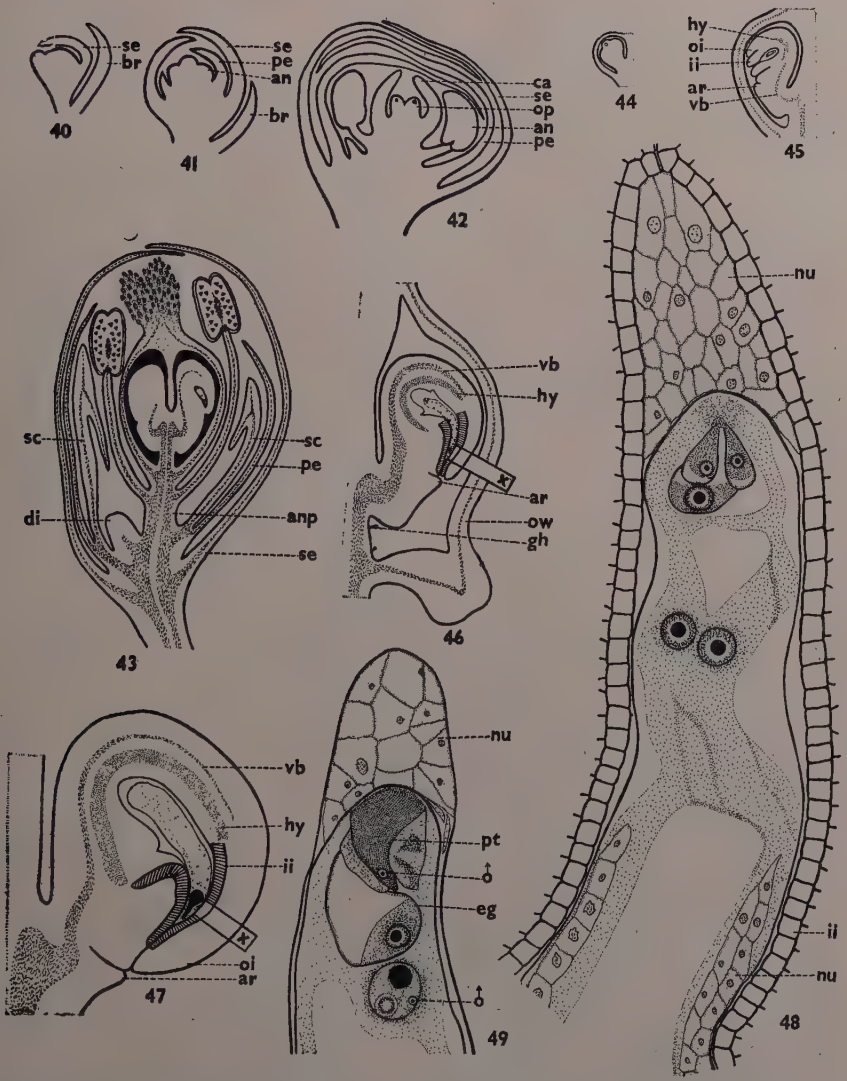
pairs to the base of the inner sepals (Text-Figs. 22–25). Each petal has a scale attached to it (Text-Figs. 25, 26, 43). There is a unilateral glandular disc attached to the base of one of the sepal-petal-triplets (Text-Figs. 22–24, 43). There are eight stamens bearing dithecous introrse anthers, borne on a small androphore (Text-Fig. 43). They are slightly connate at the base. The four nearest to the glandular disc are shorter than the rest. In the functionally female flower the anther lobes contain sterile pollen grains. The staminate flower is provided with a carpellode. The gynœcium in the bisexual and female flower is tricarpellary with an ovule for each carpel (Text-Figs. 35–37). It is three-celled at the base but in the higher regions the placentas recede to the periphery (Text-Fig. 38). The short style has three glandular stigmas (Text-Fig. 43).

The floral parts are covered with unicellular hairs (Text-Figs. 14–15). There are multicellular glands on the inner wall of ovary, septum and placenta (Text-Fig. 46). A gland arises as a small papillate protuberance (Text-Fig. 9); it elongates and divides by a transverse division to form two cells. The basal cell divides repeatedly and forms the multicellular stalk of the gland. The terminal cell divides by two vertical divisions at right angles to each other and becomes the gland (Text-Figs. 10–13).

The floral primordium arises in the axil of a bract and the floral organs develop in acropetal succession (Text-Figs. 40–42).

VASCULAR ANATOMY OF THE FLOWER

Male Flower.—The collateral vascular bundles in the pedicel divide to form four bundles in the receptacle from which diverge four traces which in turn divide into three each (Text-Figs. 16–18). The lateral branches of adjacent traces fuse to form a cylinder of vascular tissue outside the original four bundles (Text-Fig. 18). The cylinder soon breaks up into eight bundles at the base of the sepals; three each form the supply to outer sepals (Text-Fig. 19). Each of the other two divides into three and enters the inner sepal after supplying a trace each to the petal from the lateral branches (Text-Figs. 20, 21). At higher regions the sepal shows five to seven bundles. The petal trace divides radially into two and they undergo another tangential division (Text-Figs. 22–25). The inner of these enter the scale and in the higher region there are five bundles each, both in the scale and in the petal (Text-Figs. 25, 26). The disc supply consists of four traces from one side of the central stele, which branch profusely and finally disappear in the higher regions of the disc (Text-Figs. 21, 22, 43). Close below the level of stamens there are twelve vascular bundles, of which eight



TEXT-FIGS. 40–49. Figs. 40–42. Organogeny, ×50. Fig. 43. L.S. flower, ×25. Fig. 44. Young ovule at megaspore mother cell stage, ×25. Fig. 45. Ovule at two-nucleate embryo-sac stage, ×25. Fig. 46. The same at free nuclear endosperm stage, ×25. Fig. 47. The same at globular embryo stage, ×25. Fig. 48. Part of ovule at mature embryo-sac stage showing nucellar cells, ×500. Fig. 49. Ovule at the time of fertilization, ×500. (*an*, stamen; *any*, androphore; *ar*, aril; *br*, bract; *ca*, carpel; *di*, disc; *eg*, egg; *gh*, multicellular gland in ovarian cavity; *hy*, hypostase; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *op*, ovular primordium; *ow*, ovary wall; *pe*, petal; *pt*, pollen tube; *sc*, scale; *se*, sepal; *vb*, vascular supply to ovule.)

diverge out and form the supply of the stamens (Text-Figs. 26–28). The remaining bundles fuse to form a triangular stele and supply the carpellode (Text-Figs. 27, 28).

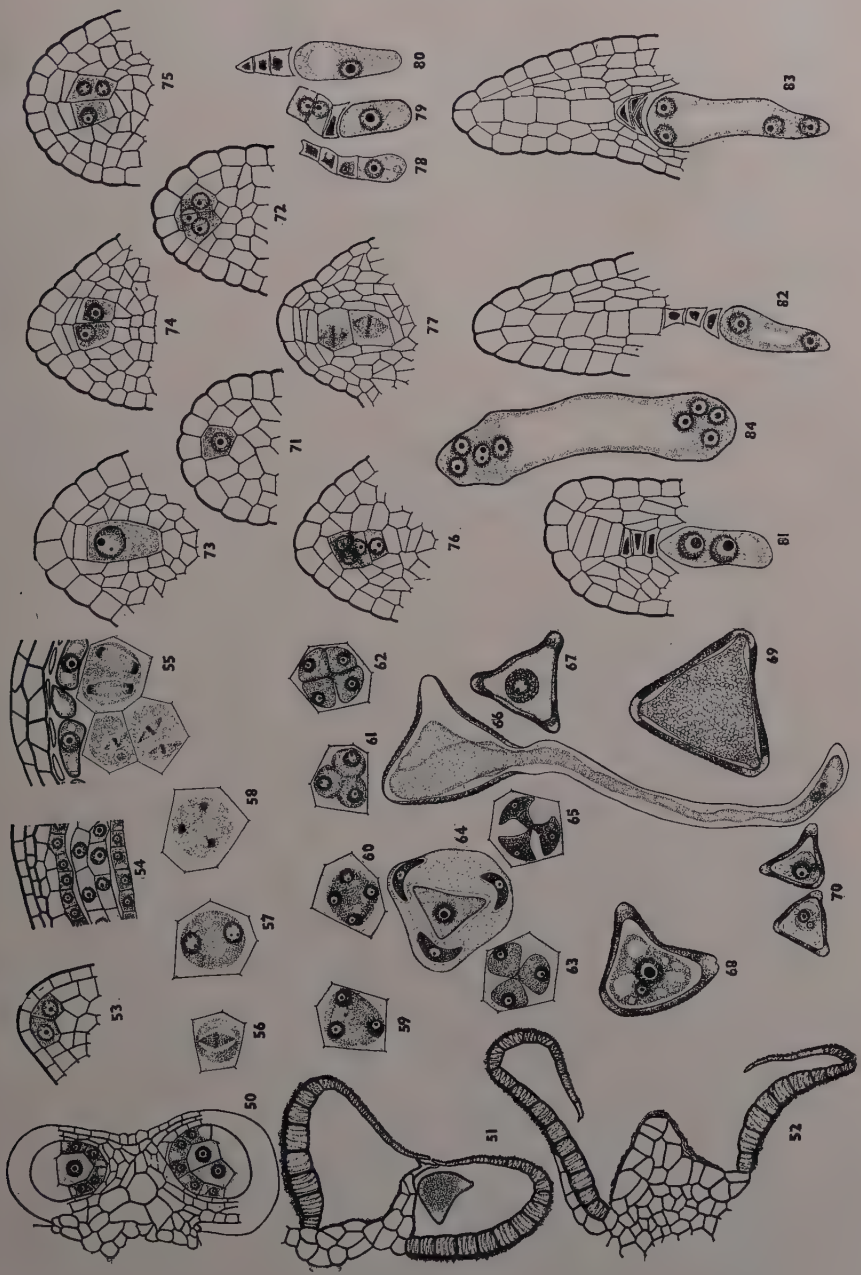
Bisexual and Female Flower.—The supplies to the sepal, petal, disc and stamens (or staminodes) are as in the male flower. From the triangular stele, above the level of stamens, diverge three traces and each divides into a dorsal and two secondary marginals on either side (Text-Figs. 29–31). The locules of the ovary appear at this level. There are three normally oriented bundles left in the centre which arrange themselves along the septal radii. From each secondary marginal separates a small bundle which moves into the septum and fuses with the inversely oriented placental bundle at a higher level (Text-Figs. 32–37). Close below the ovular region, each normally oriented bundle divides into two and fuse in pairs opposite the dorsal bundles to supply the ovules (Text-Figs. 33–36). After the ovular supply the inversely oriented bundles divide again into two each. The adjacent bundles fuse in septal radii and the resulting bundles are inversely oriented (Text-Fig. 37). The septa recede slightly to the periphery at this level. At the base of the style the inversely oriented bundles again divide into two each. They fuse with the secondary marginals, and with the dorsal bundles form the supply of the style (Text-Fig. 39). Finally they fade towards the stigma.

Microsporangium and Male Gametophyte

The young anther of the staminate flower is four-lobed. A hypodermal archesporium of two to three rows of cells is distinguished in each lobe (Text-Fig. 53). The primary parietal layer cut off by the archesporium divides to form four layers of cells beneath the epidermis (Text-Fig. 54). The subepidermal layer develops into the endothecium, whose cells elongate radially and become thickened; the characteristic fibrous thickenings develop only after the uninucleate pollen grains are formed in the microsporangium (Text-Figs. 51, 52).

The inner wall layer functions as the uninucleate tapetum (Text-Figs. 50, 54, 55) of the secretory type. The middle layers are crushed and absorbed. The primary sporogenous cells function directly as spore mother cells and develop new wall inside the original mother cell-wall (Text-Fig. 56). They undergo two meiotic divisions in a simultaneous manner (Text-Figs. 57–60). The spindles of the second meiotic divisions are at right angles or parallel to each other (Text-Fig. 55), giving rise to tetrahedral or isobilateral tetrads (Text-Figs. 61–63). The tetrahedral arrangement is more common. Quadruplication takes place by centripetal furrows (Text-Fig. 61). Degeneration of tetrads is common in the female and bisexual flowers (Text-Fig. 65). Text-Figure 64 shows a tetrad in which all cells except one are degenerating. Finally, the microspores acquire their own walls.

The young microspore is triangular and has three germpores (Text-Fig. 69). The pollen grains are shed at the two-celled stage (Text-Fig. 68). At the time of shedding they contain abundant reserve



TEXT-FIGS. 50–84

TEXT-FIGS. 50–84. Figs. 50–52. Young and old anther lobes showing cellular details at the region of dehiscence. Fig. 50, ×188. Figs. 51, 52, ×169. Fig. 53. Hypodermal archesporium in anther, ×375. Fig. 54. Part of anther in L.S. showing wall layers and microspore mother cells, ×375. Fig. 55. Part of anther at the time of second meiotic division, ×375 Figs. 56–63. Microsporogenesis and tetrads, ×375. Fig. 64. Microspore tetrad with three degenerating spores, × 375. Fig. 65. Degenerating tetrad, ×375. Fig. 66. Germinating pollen grain from the stigma, ×375. Figs. 67-68. Uninucleate and two-celled pollen grains × 375. Fig. 69. Whole mount of pollen grain, ×375. Fig. 71. Hypodermal archesporium. Fig. 72. Multicellular archesporium. Figs. 73–76. Megaspore mother cells beneath varying number of parietal layers. Figs. 77–80. Second meiotic division and megaspore tetrads. Figs. 81–84. Development of embryo-sac. Figs. 71–84, ×375.

food. The mature grain has a thick exine and a thin intine. Degeneration of pollen grains is common. Anthers of female flowers also produce two-celled pollen grains but these in comparison to male and bisexual flowers are very small, stain lightly, and are sterile (Text-Fig. 70).

At maturity partition wall between microsporangia breaks down (Text-Figs. 50–52). The mature anther wall consists of only the fibrous endothecium and remnants of epidermis. Dehiscence takes place at the junction of pollen sacs where the cells are narrow, elongated, and have poorly developed fibrillar thickenings (Text-Figs. 51, 52).

MEGASPORANGIUM AND FEMALE GAMETOPHYTE

There is a bitegmic crassinucellate ovule in each locule. The ovular protuberance is erect at the megaspore mother cell stage; soon it curves and becomes anatropous (Text-Figs. 44, 45). In later stages, the nucellus and the embryo-sac become curved and during post-fertilization stages there is a rapid division of cells at the chalazal region on the side away from the funicle, resulting in a campylotropous condition (Text-Figs. 46, 47, 119). The inner integument develops first, at the megaspore mother cell stage. The outer follows soon (Text-Figs. 44, 45). The micropyle is formed by the inner integument (Text-Fig. 45). The vascular strand supplying the ovule can be marked out at the megaspore tetrad stage and in the chalazal region it divides into a number of branches which extend to the base of the integument. These strands traverse in the outer integument and become very prominent during post-fertilization stages (Text-Figs. 45-47, 119, 129). A group of cells in the chalazal end of the ovule stain deeply and may be regarded as a hypostase (Text-Figs. 45–47). It becomes conspicuous during post-fertilization stages.

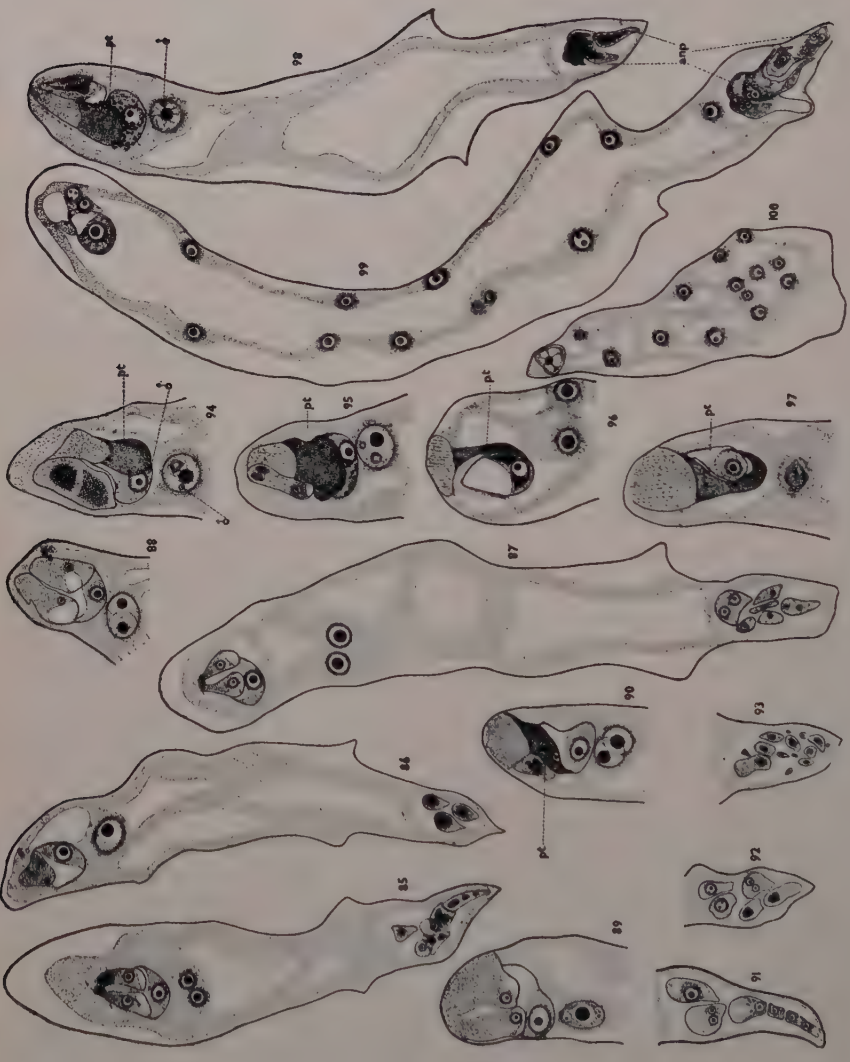
Usually a single hypodermal archesporial cell is differentiated in the nucellus (Text-Fig. 71); sometimes there are two to four (Text-Fig. 72). They lie side by side or one below the other, and usually only one develops further. Occasionally all develop into megaspore mother cells after cutting of parietal cells (Text-Figs. 74–76). However no case of twin embryo-sacs was observed. The megaspore mother cell undergoes the usual reduction divisions to produce a linear tetrad of megaspores (Text-Figs. 77–80). At the tetrad stage

there are four to six parietal layers. Of the four megaspores the chalazal functions (Text-Figs. 78, 80, 81). The others degenerate from the micropylar end downwards. In one case the third megaspore was found to degenerate earlier than the upper two megaspores (Text-Fig. 79). Degeneration of megaspore mother cells and tetrads is frequent. The functioning megaspore enlarges, becomes vacuolated, undergoes three successive divisions to produce an eight-nucleate embryo-sac (Text-Figs. 81–84), of the Polygonum type (Maheshwari, 1950).

During the development of the embryo-sac it consumes the nucellar cells on the sides and comes in contact with the inner integument (Text-Fig. 48). But an integumentary tapetum is not differentiated. At the mature embryo-sac stage, there are about eight to nine layers of nucellar cells (Text-Figs. 48, 49) in the micropylar region and they are consumed during post-fertilization stages. The mature embryo-sac is curved. During post-fertilization stages the chalazal end of the embryo-sac becomes broader and aggressive (Text-Figs. 46, 47). The synergids are hooked, have basal vacuoles and apical nuclei (Text-Figs. 88). The egg is flask-shaped, hangs down slightly beneath the synergids, and has cytoplasm and nucleus in the basal part and vacuole in the upper. The polar nuclei meet in the centre of the sac, move up and take a place close below the egg apparatus where they fuse to form a secondary nucleus long before fertilization (Text-Figs. 85–89). But in one case the polar nuclei had not fused although the pollen tube had entered the embryo-sac (Text-Fig. 90). Usually the antipodals are more than three and as many as fourteen cells have been observed (Text-Figs. 85–87, 91–93). They form a very conspicuous structure in the mature embryo-sac. Multinucleate condition of the antipodals is very frequent (Text-Figs. 91, 92, 99). They persist even after fertilization up to the three- or four-celled proembryo stage and degenerate afterwards.

Pollination and Fertilization

The flowers are entomophilous and open at night. Bisexual flowers are protandrous and cross-pollination is the rule. Germinating pollen grains have been observed on the glandular stigma. In one case pollen grains were found germinating in one of the anther lobes of an open flower. The pollen tube comes out through one of the germ pores (Text-Fig. 66), traverses the style and finally enters the ovule through the very narrow micropyle. The sperms could not be marked out in the tubes traversing the styles. Fertilized embryo-sacs possess only one synergid, the other being presumably destroyed during the process of fertilization (Text-Figs. 49, 94–98). The persisting synergid and the remnants of the destroyed synergid, if present, are absorbed soon. However in one embryo-sac with a four-celled embryo two disintegrating synergids were observed (Text-Fig. 107). The pollen tube inside the embryo-sac shows certain structures varying in number, shape and size. They stain darkly and become a very conspicuous feature of fertilized embryo-sacs (Text-Figs. 94–98). These



TEXT-FIGS. 85–100

TEXT-FIGS. 85–100. Figs. 85–87. Embryo-sacs. Figs. 88-89. Part of embryo-sac showing egg apparatus and secondary nucleus. Fig. 90. Embryo-sac at time of fertilization, the polar nuclei have not fused. Figs. 91–93. Chalazal ends of embryo-sacs showing number of antipodals. Figs. 94–98. Stages in fertilization. Figs. 99, 100. Zygote and free nuclear endosperm. All figures, ×300. (*anp*, antipodals, *pt*, pollen tube.)

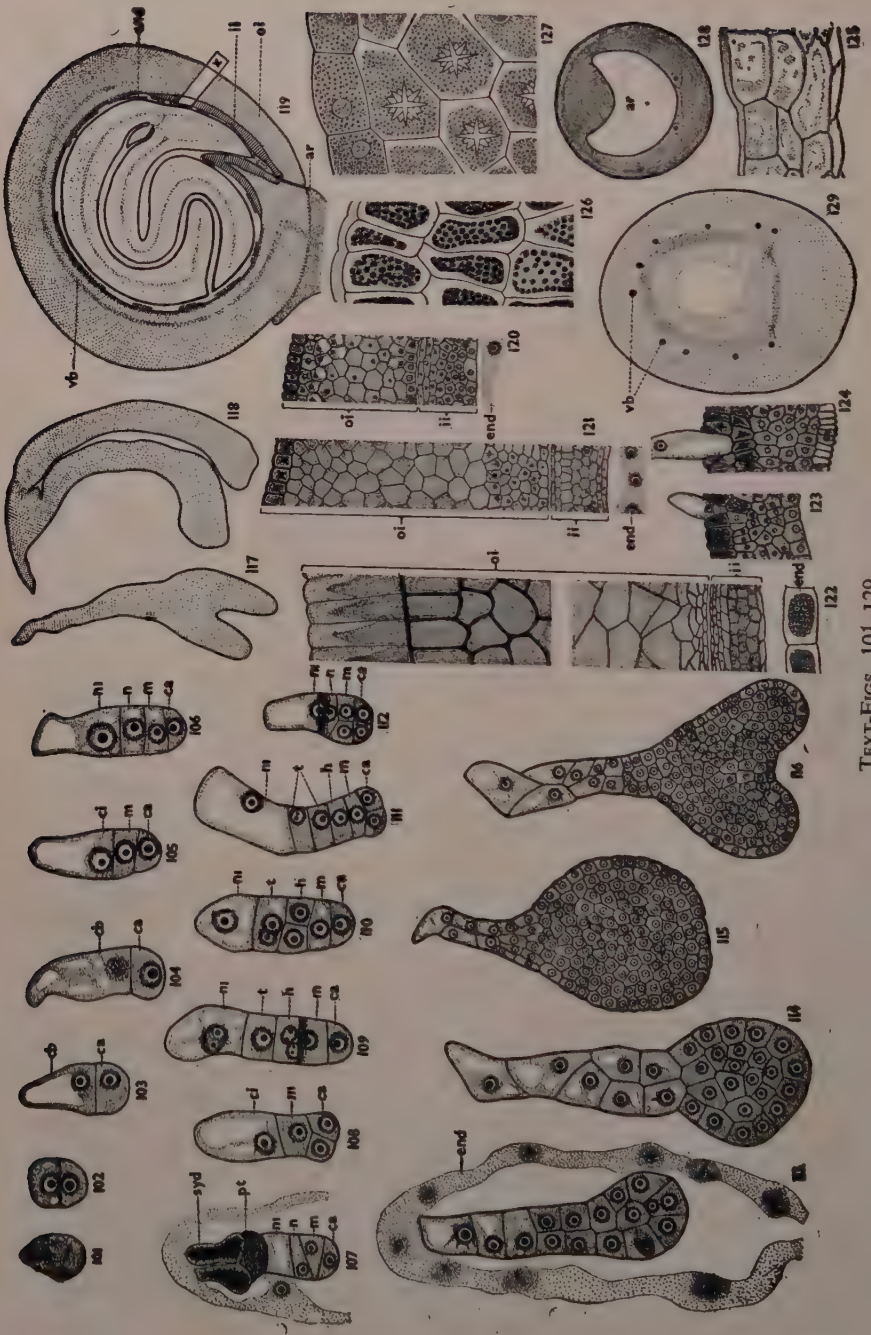
structures may correspond to the X-bodies reported in some plants (*see* Maheshwari, 1950). The end of the pollen tube is often broad and becomes a cap-like structure fitting upon the egg. Sometimes remnants of the pollen tube may persist during early stages of embryo development (Text-Fig. 107). Syngamy and triple fusion have been observed in a number of cases and they occur almost simultaneously. The male cells are spherical.

ENDOSPERM

The primary endosperm nucleus divides earlier than the zygote (Text-Figs. 96, 97, 99, 100). The development of the endosperm conforms to the free nuclear type. The large number of nuclei formed by the synchronous division of the endosperm nuclei get distributed along the peripheral cytoplasm (Text-Fig. 113). The developing embryo consumes the endosperm and in a mature seed one or two layers of cellular endosperm are found at certain regions of the seed (Text-Fig. 119). The persisting endosperm cells have thin walls and granular contents (Text-Fig. 122).

The zygote divides transversely to produce a terminal cell *ca* and a basal cell *cb* (Text-Figs. 101–103). The basal cell *cb* undergoes transverse division to give rise to cells *m* and *ci* (Text-Figs. 104, 105, 108); *ci* undergoes another transverse division to form *n* and *nl* (Text-Figs. 106, 107, 112). While *nl* does not divide further, the cell *n* divides again to produce *h* and *t* (Text-Figs. 109, 110). By the division of the latter a row of cells is produced (Text-Figs. 111, 113). The derivatives of *t* divide vertically and along with *nl* form the suspensor (Text-Figs. 113–116). The cell *h* divides vertically. The cell *m* divides longitudinally either before or after the division of *n* to form *t* and *h* (Text-Fig. 112). The terminal cell *ca* divides vertically or by an oblique wall (Text-Fig. 108). The first division of *ca* may take place at the three-celled stage (Text-Fig. 108) or it may be delayed till five tiers of cells are formed from *cb* (Text-Fig. 111). The derivatives of *ca* with those of *h* and *m* give rise to the embryo.

The large mature embryo has two unequal, fleshy cotyledons (Text-Figs. 116–119). The tip of the shorter cotyledon is fitted into a loop formed by the other (Text-Fig. 119). The embryo shows vascular strands from hypocotyl into cotyledons. The seed contains only one embryo and no case of polyembryony has been observed. The body of the embryo consists of polygonal cells which are closely packed with food grains and oil globules so that their nuclei cannot be easily distinguished. A remarkable feature is that most of these cells contain large sphærocrystals (Text-Fig. 127).



TEXT-FIGS. 101–129

TEXT-FIGS. 101–129. Figs. 101–116. Stages in development of embryo. Figs. 101–114, × 375; rest, × 188. Figs. 117-118. Embryos. Fig. 117, × 82. Fig. 118, ×37·5. Fig. 119. L.S. seed, ×9. Figs. 120–122. Stages in development of seed coat. Enlarged portions marked X in Figs. 46, 47 and 119 respectively, ×188. Figs. 123–125. Stages in development of pericarp, ×188. Fig. 126. Part of aril enlarged, ×188. Fig. 127. Part of cotyledon enlarged to show the food contents and sphærocrystals, ×375. Fig. 128. Face view of mature seed, ×5. Fig. 129. T.S. seed showing vascular bundles in seed coat, ×37·5. (*ar*, aril; *end*, free nuclear endosperm; *ii*, inner integument, *oi*, outer integument; *pt*, pollen tube, *syd*, synergid, *vb*, vascular bundle in seed coat.)

It is thus seen that the embryo proper is formed from the derivatives of both the terminal and basal cells *ca* and *cb* of the two-celled proembryo and hence it follows the Asterad type.

SEED COAT

After fertilization there are about nine to ten layers of cells in the outer integument and six to seven layers in the inner integument (Text-Fig. 120). In later stages there is a pronounced growth in the chalazal region. The outer integument becomes 19–20 cells thick (Text-Figs. 121, 122). The cells contain tannin. The outermost two to three layers of cells are thick-walled and the innermost three layers of narrow cells are thin-walled. The inner integument does not undergo much change. The middle two to three layers of tannin-bearing cells become very conspicuous while the others are narrow due to tangential elongation (Text-Fig. 122). The coat of the globose black seed is very hard. There are two small depressions on the seed coat below the convex side of the aril (Text-Fig. 128).

ARIL

At about the two-nucleate stage of the embryo-sac a protuberance arises at the base of the ovule (Text-Fig. 45). This becomes very conspicuous during post-fertilization stages and envelopes part of the mature seed (Text-Figs. 46, 47, 119, 128). The white kidney-shaped aril is composed of parenchymatous cells containing large amount of deep staining granular contents (Text-Fig. 126).

FRUIT

The trilocular three-seeded fruit is an inflated septifragal capsule. The pericarp which is five- to six-layered during earlier stages becomes eight- to nine-layered after fertilization (Text-Figs. 123, 124). At the time of dehiscence the membranous capsule wall consists of four layers of cells (Text-Fig. 125) and dehiscence takes place septicidally.

DISCUSSION

Hooker (1875), Duthie (1903), and Kirthikar and Basu (1933) state that the leaves of *C. halicacabum* are exstipulate. But the leaves examined in the present study have two scale-like stipules. The nodal anatomy of *Cardiospermum* is trilacunar. Sinnot and Bailey (1914)

observed, that, in general, the stipular supply of members possessing trilacunar nodes is associated with the lateral traces. *Cardiospermum* is essentially similar.

According to Metcalfe and Chalk (1950) there are only four bundles in the petiole of *Cardiospermum*. But in our material the petiolar supply consists of four large and four small vascular bundles.

The cirrhose tendrils of the inflorescence have been described as modified pedicels in current taxonomic works, text-books, and manuals (Hooker, 1875; Duthie, 1903; Bamber, 1916; Dutta, 1952). Mitra (1957) has described it as a metamorphosed peduncle. While the pedicel receives only two bundles from the central stele the tendril, like the branches of the inflorescence, receives three bundles which divide to form a large number of bundles. On this basis the tendrils are regarded modified lateral branches of the inflorescence.

The inflorescence in this species is described as an axillary raceme (Hooker, 1875; Bamber, 1916), axillary racemes or corymbs (Chopra *et al.*, 1949), small cymes terminating in a long stiff slender axillary peduncle (Duthie, 1903), umbellate cymes (Kirthikar and Basu, 1933), and umbel-like cymes (Mayuranathan, 1929). According to the definitions of Rickett (1944, 1955) none of the above terms are applicable to the inflorescence of *C. halicacabum*. As has been shown earlier the main axis of the inflorescence divides into three at the tip; each bears two rows of four to five flowers on one side. That the sterile bracts of the inflorescence were fertile is being indicated by the occasional presence of undeveloped primordia in their axils. On this basis it is suggested that the branches of the original inflorescence had a decussate arrangement of flowers and during evolution two rows of flowers on one side had been suppressed. The inflorescence is, therefore, regarded to be a reduced panicle (*cf.* Rickett, 1955).

The vascular supply shows adnation among members of the same whorl and between adjacent whorls of perianth lobes. The present study does not support Saunders' (1939) statement that the tetramerous nature of the outer whorl of perianth is derived from a pentamerous condition by the fusion of the third and fifth sepals. Similarly her contention that one of the petals is suppressed from the original five is not substantiated. Each petal is provided with a bilobed scale attached to its base. The position and vascular supply indicates that the scale is an outgrowth of the petal.

The disc receives four traces from one side of the receptacular stele and this shows its receptacular nature.

After the dorsal and secondary marginal traces have diverged there are three normally oriented bundles in the centre which extend up to the middle of the ovary. In the ovule-bearing region they divide into two each and fuse in pairs to form three inversely oriented bundles which function as placental bundles. The question is what is the

nature of the central bundles till they become placental strands; are they stelar or carpellary? The change in orientation gives the clue for the morphological nature of these bundles. Similar changes in the orientation of the bundles are known in other plants (Puri, 1952). The normal orientation of the bundles below the ovule-bearing region indicates that it is at this level the axis terminates and the carpels begin as far as the central portion of the ovary is concerned. Therefore these bundles are stelar and not carpellary. It must also be said that the axis can continue between the peripheral organs.

The placentation in the ovule-bearing region is axile since the ovary is multilocular and the placental bundles are in dorsal radii (*cf.* Puri, 1952). Close above they divide into two each and two similar bundles fuse along the septal radii. This indicates that the placentation is tending towards a parietal condition.

Kadry (1946) mentions that the primary archesporial cell cuts off a parietal layer. However his Figure 4 stated to be showing a linear tetrad of megaspores has no parietal layers. In all our preparations there were invariably 4–6 parietal layers above the tetrad. In view of the present findings Kadry's Figure 4 shows a megaspore mother cell below three parietal layers and not a linear tetrad of megaspores.

According to Mauritzon (1936) the antipodals in most genera are ephemeral. Kadry (1946) makes contradictory remarks with regard to the time of degeneration of antipodal cells in *Cardiospermum.* On page 114 he writes that the antipodals disintegrate soon after the division of the zygote. A little later (page 119) he states that the antipodals begin to disintegrate when the synergids are in the course of absorption and the primary endosperm nucleus begins to divide. We have seen the antipodals persisting up to the four-celled stage of the embryo. During post-fertilization stages the antipodals take a very deep stain and become conspicuous. Kadry (1946) observed only three antipodal cells. Increase in the number of antipodal cells is almost a common phenomenon in our material. The maximum number of cells counted is fourteen.

Citing Fig. 15 *a, b** Kadry (1946) writes "after the organization of the embryo-sac, the cells at the tip of the nucellus and some of the cells of the inner integument, which encircle the micropyle, form a mucilaginous mass through which the pollen tube enters..... The inner integument is now completely fused with the apical part of the nucellus, forming the mucilaginous tissue which extends till it nearly touches the aril". This is in contrast to the observations of Guérin (1901). We could not confirm the reports of Kadry (1946) as to the fusion of nucellar cells with inner integument and their mucilaginization. A

* This figure represents part of the longitudinal section of a fruit and is presented to prove the absence of micropylar canal. It must be mentioned that the cells of the integuments, during post-fertilization stages, come into intimate contact with each other and therefore a micropyle is not perceptible.

narrow micropylar canal and 8–9 layers of parietal cells were observed in several ovules at the time of fertilization (*see also* David, 1938).

The description of male cells by Kadry (1946) deserves closer examination. He writes "The male nucleus that fuses with the egg nucleus has a characteristic shape of one rounded head-like and one tapering end..... Its length is about four times the diameter of the polar male nucleus which is more or less spherical (Fig. 20). Thus there is a distinct and enormous difference in size and shape between male nuclei". Maheshwari (1949, 1950) has reviewed the literature on the dissimilarity in the male gametes released by a single pollen tube. According to him the reported differences in size may be due to the plane of sectioning and as pointed out by Gerassimova (1933) due to a "different tempo" in their transformation and maturation. He (1949) also feels that the difference in size and shape of the two male gametes discharged by a single pollen tube may be variations which have no special significance. In our preparations both the sperm cells were spherical and therefore we could not confirm the reports of Kadry (1946).

An accessory pollen tube with undischarged gametes has been observed by Kadry (1946). None of our preparations showed this feature.

According to Kadry (1946) the fusion of the egg nucleus with the male gamete takes place after the formation of the initial endosperm nucleus and they become completely fused only after the eight-nucleate stage of endosperm. Our observations however show that syngamy and triple fusion are almost simultaneous.

The development of the endosperm is free nuclear as reported earlier. Mauritzon (1936) stated that in some members of Sapindaceæ no wall formation of the endosperm took place even when the embryo was almost fully developed. He, however, noticed a single layer of cellular endosperm in *Cardiospermum halicacabum*. According to Kadry (1946) the endosperm is nucleate even when the embryo is fully developed. In our material the mature seed invariably showed one or two layers of cellular endosperm at certain places.

The division of zygote is transverse. Kadry (1946) states that the terminal cell divides vertically and by further divisions gives rise to the embryo while from the basal cell a suspensor is formed. Accordingly the development of the embryo would fall under the Onagrad type (Johansen, 1950). Our study of the embryo development shows that the embryo is formed from both the basal and the terminal cells of the two-celled proembryo and hence follows the Asterad type. The suspensor is biseriate with a large basal cell.

Summary

The present study deals with the morphology and embryology of *Cardiospermum halicacabum*. The biternate compound leaves are

alternate and have two scale-like stipules. The nodal structure reveals a trilacunar condition. The petiole is supplied by eight vascular bundles.

On anatomical grounds the cirrhose tendrils of the inflorescence are regarded lateral branches of the paniculate inflorescence.

The scales on the petals are regarded to be outgrowths. The unilateral and glandular disc is attached to one of the sepal-petal triplets and is considered to be receptacular in nature.

The placentation is axile in the ovule-bearing region becoming parietal above.

The anther wall consists of epidermis, fibrous endothecium, two middle layers, and a secretory uninucleate tapetum. The triporate psilate pollen grains are shed at the two-celled stage.

The embryo-sac is of the Polygonum type. The number of antipodals vary from 3–14 and are mostly multinucleate.

Double fertilization occurs and the primary endosperm nucleus divides earlier than the fertilized egg. The endosperm is of the nuclear type. In the mature seed one or two layers of cellular endosperm is present at certain places. The development of the embryo conforms to the Asterad type. The suspensor is biseriate. The embryo is dicotyledonous and the cotyledons are unequal. Their cells contain sphærocrystals and reserve food.

Both the integuments take part in the formation of the seed coat. A small kidney-shaped parenchymatous aril covers part of the seed in the micropylar region.

In conclusion the authors are thankful to Professors P. Maheshwari for lending some literature, V. Puri, for suggestions with regard to certain points and encouragement, and B. N. Mulay for facilities and help.

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OCCURRENCE OF SPERMOGONIA IN *PHYLLACHORA ACTINODAPHNES*

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Received for publication on February 25, 1959

Introduction

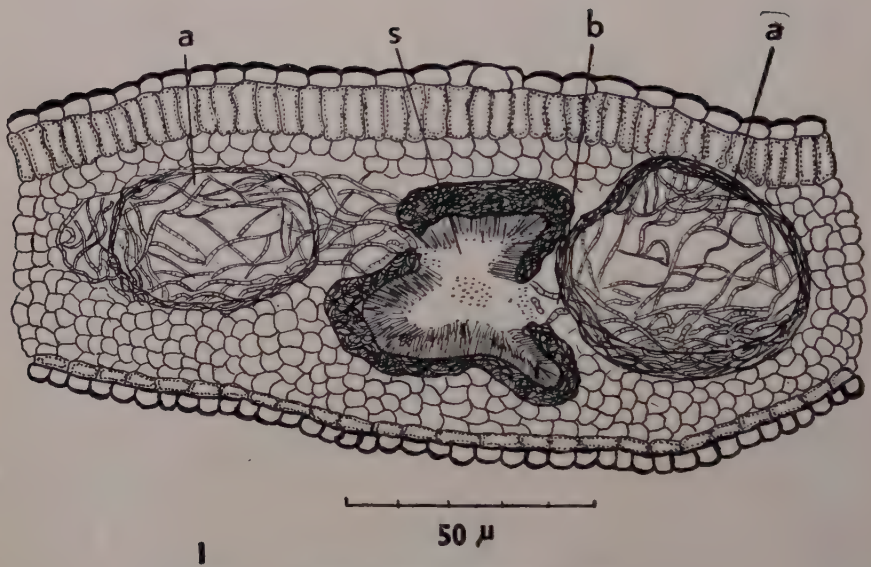
Since the classical researches of Higgins (1920, 1929, 1936) on the occurrence of spermogonia and function of spermatia in the ascomycetous fungi, many reports have been published on the presence of these bodies in several perithecial and apothecial genera and their function in the initiation of the sexual phase through the process of spermatization. Recently Miller (1954) reported spermogonia in *Phyllachora lespedezæ* (Schw.) Sacc. In the course of his studies on the Indian Phyllachoraceæ, the author had occasion to make some interesting observations in *Phyllachora actinodaphnes* Uppal, Patel and Bhide on *Actinodaphne hookeri* Meissn. A preliminary report is presented in this short note on this aspect of study.

Material and Methods

The observations were made on fresh material obtained from Mahabaleshwar during the months of January–February 1958 and fixed in F.A.A. and Navashins fixative stained with iron alum Hæmatoxylin and counterstained in orange G and light green in clove oil as described by Sass (1951).

Observations

The spermogonia in *Phyllachora actinodaphnes* are globular, thick walled, deep seated in mesophyll tissue, non-ostiolate invariably and closely associated with the young developing ascocarps on one or both sides (Plate V, Fig. 1 *a* and Text-Fig. 1 *a*). On the inner wall of the spermogonium are produced closely packed bristle-like pointed spermatiophores with bulbous bases, from the tips of which minute rod-shaped spermatia are extruded into the central cavity. An interesting feature, not so far reported in literature, is the manner of dehiscence developed by the spermogonia in this fungus for releasing its spermatia. In the absence of a predetermined apical pore so commonly described by previous workers, an ingenious method of release of its spermatia has been developed in this fungus. The spermogonium distends laterally in the direction of the developing ascocarps and breaks open at the point of contact



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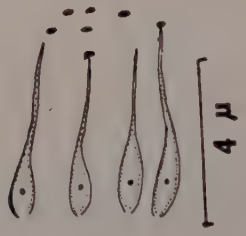
Text-Fig. 1. Camera lucida drawing of Plate V, Fig. 1.



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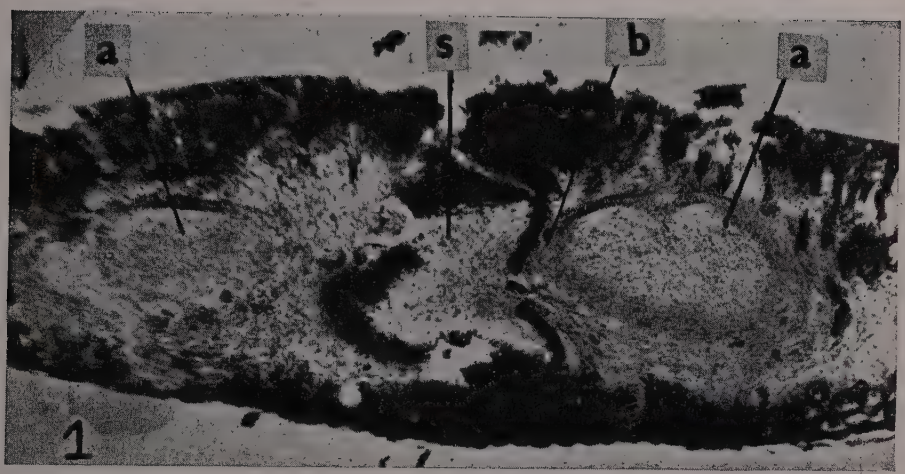
Text-Fig. 2. Spermatiophores and spermatia.

with the ascocarp initial (Plate V, Fig. 1 *a* and Text-Fig. 1 *a*). The spermogonia which are initially globular, thus, assume an ovoid shape due to the lateral distension and breakage of its walls and make way for the release of the spermatial bodies.

General Discussion

It may be mentioned here that no direct evidence has been obtained of actual sexual fusions between the spermatia and ascogonium or hyphal cells of the ascocarp initials. It was, however, significant to observe that in none of the numerous specimens and slides examined has the ascocarp development been found to take place without the close association of spermogonial bodies.



S. T. Tilak FIG. 1

The observations recorded above are of special significance and possibly denote the occurrence of spermatization in this fungus. Further work is in progress in this direction and will be presented in a subsequent report.

Acknowledgements

Grateful thanks are due to Prof. M. N. Kamat for his guidance and encouragement in the course of studies and to Dr. S. P. Agharkar for facilities offered at this laboratory.

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Explanation of Plate V

Fig. 1. Photomicrograph of Spermogonium (*s*) and developing Ascocarp initials on either side (*a*) and cleavage in lateral walls (*b*), ×400.

FOSSIL DICOTYLEDONOUS WOOD OF LECYTHIDACEÆ FROM THE DECCAN INTERTRAPPEAN BEDS OF MAHURZARI

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(Received for publication on May 11, 1959)

The present paper deals with a fossil dicotyledonous wood collected by me on the 7th June 1958 from Mahurzari, a village about 8 miles north-west from Nagpur proper. Besides silicified woods which dominate the landscape, hardly any other organic remains have so far been found at this place. These silicified woods occur firmly embedded, but a large number of them lie scattered in the fields. This is the third fossil wood to be described from this locality. The first described by me was referred to family Burseraceæ (Shallom, 1958), and the second to the family Simarubaceæ (Shallom, 1959).

To my knowledge, fossil wood of the family Lecythidaceæ (now separated from the family Myrtaceæ) has not so far been reported from India. Even from outside India there has not been any record of this family, though fossil woods of Myrtaceæ have been described both from India (Uttam Prakash, 1956) and abroad (Chapman, 1918; Warren, 1912).

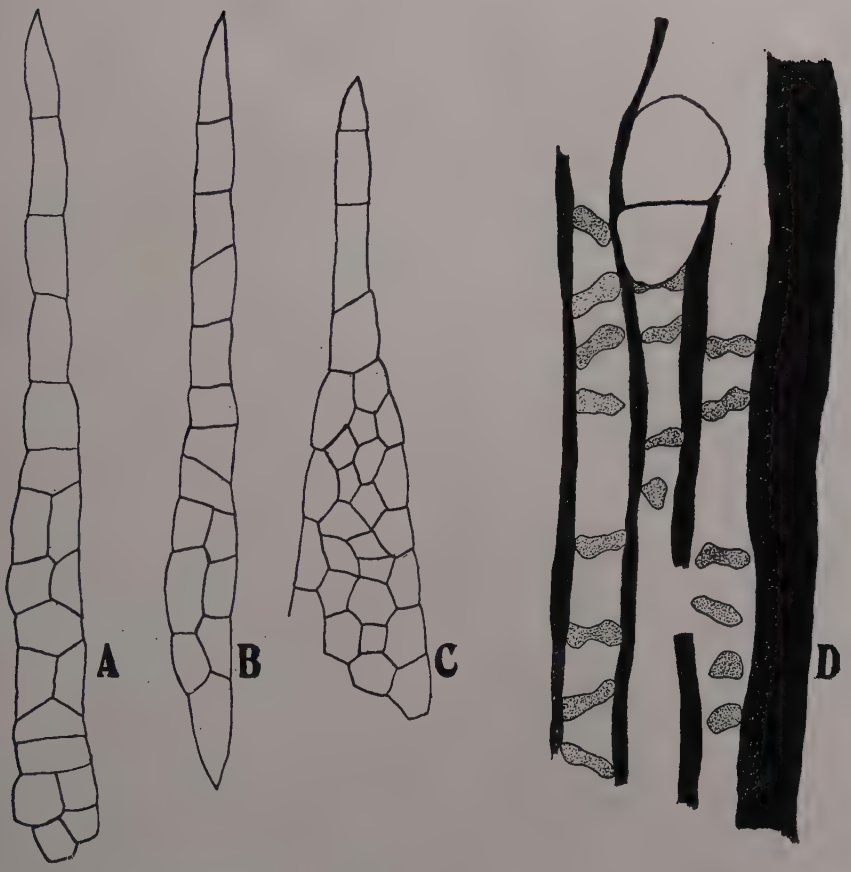
The preservation of the present material is fairly good, the brown petrifactions of the same has made it possible for me to study the wood in complete detail with consequent comparisons with the modern timbers. Several transverse, tangential and radial sections were made of this wood, and all were studied after mounting them in Canada-balsam. Peel sections were also tried but without any success.

Description

The wood under investigation is a highly silicified piece with colour ranging from white to dark-brown.

The fossil wood does not show any growth rings, either to the naked eye or under the microscope.

Vessels are small to medium sized. The orifices, being barely visible to the naked eye, have radial and tangential diameters varying from 100–150 μ and 78–100 μ respectively. The vessels are frequently associated with rays contiguous on one or both sides (Pl. VI, Figs. 1 and 6). Vessel segments are short varying from 200–411 μ, rather thin



TEXT-FIG. 1. A–D. *Barringtonioxylon deccanense* gen. et sp. nov.

A, B and C. Multiseriate rays with uniseriate margins of erect cells, ×210. D. Semi-diagrammatic cross-section showing the distribution of parenchyma (stippled), ×135.

to moderately thick-walled. The majority of vessels are solitary or in radial rows of 2–4 (mostly 2–3) (Pl. VI, Figs. 1 and 6). The vessels in this case are mostly filled with tyloses (Pl. VI, Figs. 3, 4, and 6). The perforation plates are exclusively simple. The intervessel pits are large and numerous with long horizontal diameters varying from 11–14 μ (Pl. VI, Figs. 2 and 7). The vessel-ray pittings are fairly numerous for each cell, oval, and usually reticulately grouped (Pl. VI, Fig. 5).

Parenchyma is paratracheal and metatracheal. Paratracheal parenchyma is sparse, mostly confined to tangential walls of the vessels. The diameter of these parenchymatous cells varies from 32–40 μ. Metatracheal parenchyma as seen in cross-section (Pl. VI, Fig. 6) is abundant and of two types: (1) Sometimes diffuse, (2) mostly in uniseriate lines

bridging the narrow gap between the adjacent rays. These parenchymatous lines are alternating with 4 rows of fibres. Cells of this parenchyma vary in diameter from 22–28 μ.

Rays are visible to the naked eye but not sharply delineated in the transverse section. They make more than half the volume of the wood. They are mostly 1–6 cells wide and heterogeneous. These rays are divisible on the basis of size and composition into two types.

(1) *Uniseriate rays.*—These are fairly abundant, consisting wholly of upright cells (Pl. VI, Fig. 2). They are 17 μ in width and 1–17 cells in height.

(2) *Multiseriate rays.*—These are 2–6 cells wide, consisting of both upright (on the flanks) and horizontal cells through the median portion, and with only erect cells in uniseriate margins, which are mostly short (Pl. VI, Figs. 2 and 3); Text-Fig. 1, A, B, and C) and occasionally elongated (Pl. VI, Fig. 2) The maximum width of these medullary rays varies from 28–100 μ while the length varies from 8–46 cells or 400–1,500 μ.

Fibres are non-libriform to semi-libriform, and more or less rounded in transverse section, and not aligned in radial rows. They form narrow stripes of fibrous tissue between the broad and the narrow rays, spanned by narrow, mostly uniseriate lines of metatracheal zonate parenchyma. The fibres are non-septate, 17–22 μ in diameter, with 3–6 μ thick walls.

Traumatic canals have been noticed in the fossil wood.

Discussion

In the absence of any outstanding character in the present fossil wood, its determination rests solely on a combination of the following characters:

1. Vessels small to medium-sized, occurring mostly solitary or in radial rows of 2–3.
2. Perforation plates exclusively simple.
3. Intervessel pits alternate, bordered and large.
4. Parenchyma both paratracheal and metatracheal as uniseriate lines, or as scattered cells.
5. Rays both uniseriate and multiseriate. Uniseriate rays mostly made up of erect cells; multiseriate rays heterogeneous; fairly broad with uniseriate margins of erect cells. Sheath cells also present.
6. Fibres thick-walled, non-libriform to semi-libriform and non-septate.

Some of these above mentioned characters bring the present specimen close to the families Tiliaceæ (Metcalfe and Chalk, 1950) and Simarubaceæ (Heimsch, 1942).

Family Tiliaceæ has some genera which show superficial resemblance to the fossil wood under consideration. But these genera markedly differ from the fossil wood in the presence of tile cells in the xylem rays, and in the presence of minute intervessel pitting.

In Simarubaceæ, *Mannia* is the only genus showing some resemblances to the fossil wood. The resemblances are found in the nature and arrangement of fibres and parenchyma. Uniseriate rays too are fairly abundant as in the fossil wood. But this genus again differs from the fossil wood in the nature of the xylem rays and of the intervessel pitting.

However, it resembles in almost all the features with the family Lecythidaceæ (Gamble, 1922; Pearson and Brown, 1932; Metcalfe and Chalk, 1950; and Diehl, 1935).

Most of the features of the fossil wood resemble those of *Barringtonia* of the family Lecythidaceæ. Transverse, tangential and radial sections of the wood of *Barringtonia acutangula* were studied both at the Forest Research Institute, Dehra Dun, and at the Science College, Nagpur.

Minor differences were observed in the presence of tyloses and traumatic canals in the fossil wood and their absence in the living timber. Tyloses and traumatic canals although not recorded in any species of *Barringtonia* are not known to be totally absent in the family.

On the above assumption, and the close resemblance shown by the fossil wood to the living timber of *Barringtonia acutangula*, particularly in the nature of vessels, parenchyma, fibres, xylem rays and intervessel pitting, the above fossil wood is placed under the family Lecythidaceæ, closest to the genus *Barringtonia*.

Diagnosis and name of the fossil wood

In view of the close resemblance of the fossil wood with that of *Barringtonia*, a new form genus *Barringtonioxylon* is created to accommodate the fossil wood. It is specifically named as *Barringtonioxylon deccanense* after the Deccan Intertrappean series from where it is collected.

***Barringtonioxylon* gen. nov.**

A diffuse porous wood.

Growth rings indistinct.

Vessels small to medium sized, barely visible to the naked eye; solitary or in radial rows of 2–3; perforations simple, horizontal; intervessel pitting large, alternate and bordered. Parenchyma both paratracheal and metatracheal; paratracheal parenchyma sparse; metatracheal parenchyma abundant, diffuse as well as in uniseriate lines.

Rays numerous, visible to the naked eye, evenly distributed, very high with uniseriate margins made up mostly of erect cells; sheath cells also present.

Fibres non-libriform to semi-libriform, non-septate and not aligned in radial rows.

***Barringtonioxylon deccanense* sp. nov.**

Vessels with radial and tangential diameters varying from 100–150 μ and 78–100 μ respectively; mostly in radial rows of 2's or 3's, angular, tyloses present; vessel segments 200–400 μ; intervessel pits alternate, diameter varying from 11–14 μ.

Parenchyma paratracheal and metatracheal; diameter of the paratracheal parenchyma cell varies from 32–40 μ. Metatracheal parenchyma cell varies in diameter from 28–32 μ, this parenchyma abundant in part scattered and mostly as uniseriate lines joining two adjacent rays. Uniseriate rays fairly abundant; 17 μ in width; 1–17 cells high; broad rays 2–6 seriate; heterogeneous, 28–100 μ in width, 8–46 cells or 400–1,500 μ high. Fibres non-libriform; non-septate, 17–22 μ in diameter, 1,000–2,300 μ in length, wall 3–6 μ thick. Traumatic canals present.

Summary VI

A new fossil wood of the family Lecythidaceæ has been described here for the first time from India. It has been named as *Barringtonioxylon deccanense* because of its striking similarities with the living genus *Barringtonia*. It has been collected from the Deccan Intertrappean beds of Mahurzari, a village about 8 miles north-west of Nagpur proper.

Acknowledgements

I am highly grateful to Dr. (Mrs.) S. D. Chitaley of Government College of Science, Nagpur, under whose kind guidance and encouragement this work was carried out, and to Mr. S. S. Ghosh and Mr. M. H. Kazmi of the Forest Research Institute, Dehra Dun, for their valuable suggestions. I am also grateful to Dr. Navalkar of the Institute of Science, Bombay, and to the Conservator of Forests, West Bengal, for the required material of *Barringtonia acutangula*.

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FIGS. 1–8

L. J. Shallom

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EXPLANATION OF PLATE VI

FIG. 1. Transverse section (magnified) showing well the nature of vessels and thickness of the fibres, ×53.

FIG. 2. Tangential section (magnified) showing the nature of the medullary rays as well as of the intervessel pits, ×53.

FIG. 3. Tangential section showing well the distribution of medullary rays and few complete multiseriate rays with uniseriate margins at both ends, ×40.

FIG. 4. Radial section showing heterogeneous condition of the medullary rays, vessels with tyloses VT, paratracheal parenchyma *pp* and metatracheal parenchyma W, ×40.

FIG. 5. Vessel ray pitting, ×40.

FIG. 6. Transverse section under low power showing clearly the distribution of parenchyma and fibres as seen in transverse section, ×45.

FIG. 7. Intervessel pits magnified, ×204.

FIG. 8. Transverse section showing the traumatic canals, ×53.

STUDIES IN BURSERACEÆ—I

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(Received for Publication on February 6, 1959)

Introduction

The family Burseraceæ comprises 20 genera and 500–600 species (Lawrence, 1951). Floral anatomy of *Canarium nitidum* (Saunders, 1939) and *Balsamodendron mukul* (Shukla, 1955) is only known so far. The present study deals with the floral anatomy of *Boswelia serrata* Roxb. and *Garuga pinnata* Roxb.

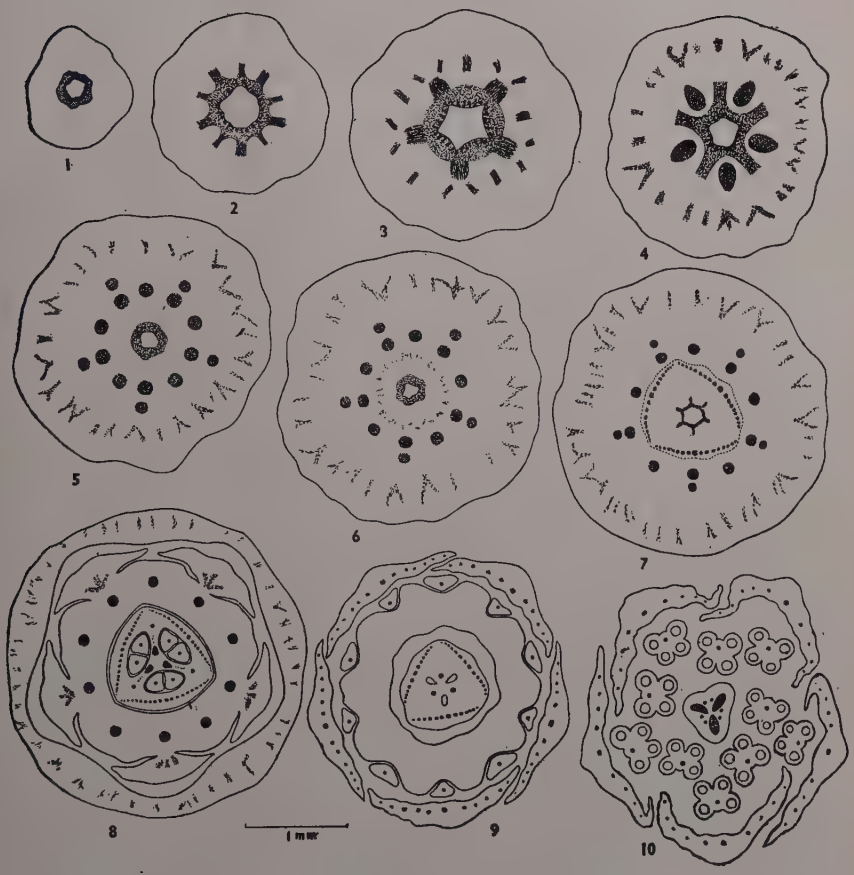
Materials and Methods

The materials were fixed in F.A.A. Usual methods of dehydration, infiltration and embedding were followed. Sections were cut at a thickness of 6–12 μ and were stained in Crystal violet with Erythrosin as counter stain.

Observations

Boswelia serrata.—The flower has two pentamerous perianth whorls of which the calyx is gamosepalous (Text-Fig. 8). The quincuncial petals are free (Text-Figs. 8–10). There are ten stamens of two heights. The ovary is tricarpellary syncarpous, trilocular with two collateral ovules in each loculus (Text-Fig. 8). The elongated style in a transverse section shows three canals lined by glandular transmitting tissue (Text-Fig. 10). The stigma bears numerous unicellular hairs. A massive lobed disc is present between the androœcium and gynœcium (Text-Fig. 9).

The pedicel shows a siphonostele (Text-Fig. 1). In the region of the thalamus ten traces arise from the main stele (Text-Fig. 2). Of these five represent the sepal midribs and these soon become detached from the main stele. The remaining five represent the conjoint traces of the sepal laterals, petal midribs and antepetalous stamens (Text-Fig. 3). From these, the common sepal laterals are demarcated as a result of tangential splitting (Text-Figs. 3 and 4). These bifurcate as they enter the base of the gamosepalous calyx. At a higher level the now common traces for the petals and antepetalous stamens separate from the main stele and alternating to them arise independently from the main stele, the traces for the antesepalous stamens (Text-Fig. 4). Thus, the androœcium in *Boswelia* may be regarded obdiplostemonous. The common petal-stamen bundles undergo tangential splitting demarcating the petal



TEXT-FIGS. 1–10. *Boswelia serrata.* (For description see text.)

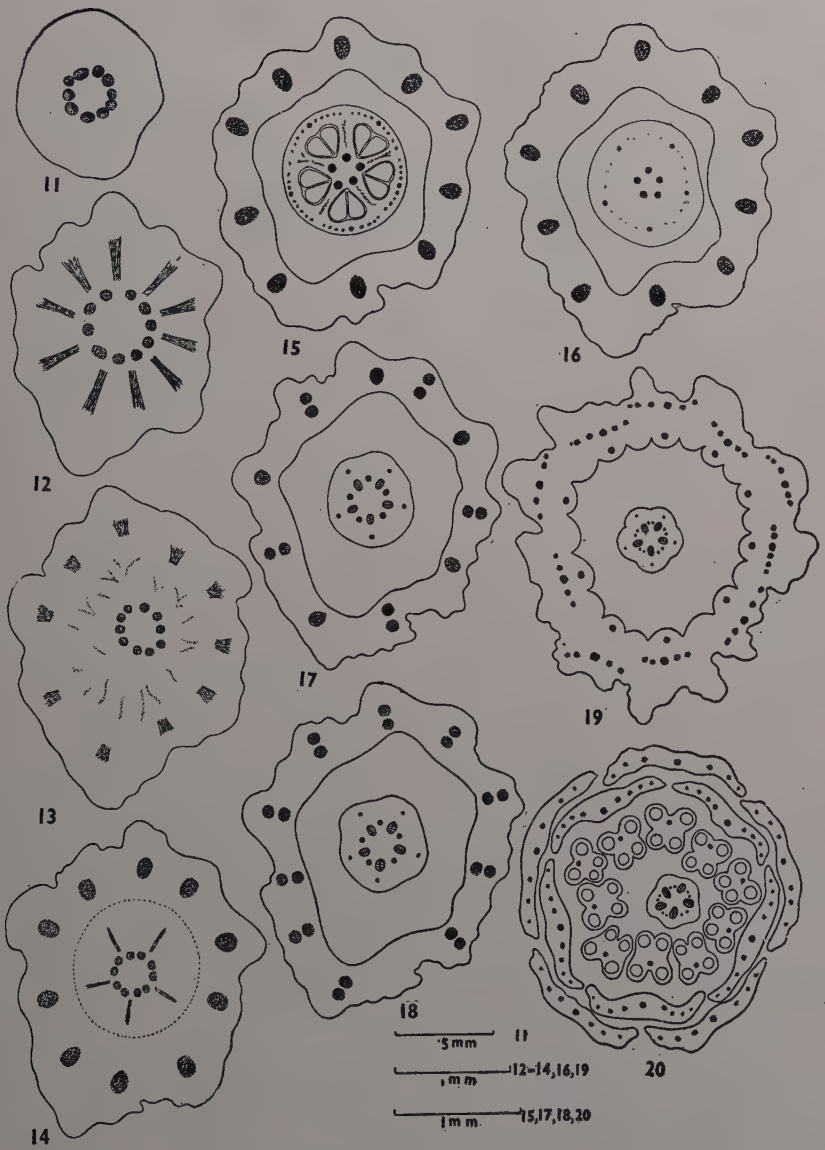
midribs towards the outside and staminal bundles towards the inside (Text-Figs. 5 and 6). Soon the antesepalous staminal bundles emerge out and all the ten staminal bundles are arranged in a ring. At this level these staminal bundles give off branches towards the inside (Text-Fig. 6). These branches, however, fade out at a higher level. At the level where the ovary separates from the floral axis six traces arise from the main stele (Text-Fig. 7). Of these, three are the dorsal carpellary traces and the remaining three are the common median laterals; the former fade out soon while the latter continue to the top of the ovary (Text-Fig. 8). The remaining part of the main stele organises into three common ventrals which lie on the septal radii (Text-Figs. 8 and 9). Branches from these supply the ovules. A few branches which traverse the septa are also given off. The ventrals continue into the style where each divides into two (Text-Fig. 10). Towards the tip, the style divides into three branches and each in turn is two lobed.

At about the level where the dorsals and median dorsals are demarcated, certain deeply staining cells which extend up for some distance are seen in the ovary wall (Text-Figs. 7–9). However, they do not continue into the style.

Garuga pinnata.—The flower has two pentamerous whorls of perianth, ten stamens and a pentacarpellary gynœcium. Adnation of the calyx, corolla and androecium results in a cup-like structure (Text-Figs. 14–19) from whose rim the respective organs separate (Text-Fig. 20). There is no disc between the androecium and gynœcium. In between the stamens, at the base, there are small cushion-like projections. The ovary is superior pentalocular with two ovules in each loculus (Text-Fig. 15). In a transverse section the style shows five canals lined by glandular transmitting tissue (Text-Figs. 17–20). The stigmatic region bears numerous hairs.

The pedicel shows a ring of vascular bundles (Text-Fig. 11). These form a ring in the thalamus from which ten traces arise causing as many gaps (Text-Fig. 12). They bend outwards towards the periphery and enter the base of the cup-like structure formed by the union of perianth members and stamens (Text-Figs. 14–19). As they emerge out they give off branches towards the inside which face in the thalamus. Of these ten bundles five represent the common bundles of the sepals and antesepalous stamens and the remaining five the common bundles of petals and antepetalous stamens. After the departure of these traces the stele forms five bundles, which in turn form a ring at a higher level. From this ring five dorsal carpellary traces arise (Text-Fig. 14). These divide and form smaller bundles as they enter the wall of the ovary. The remaining part of the stele forms five common ventral bundles which lie on the septal radii (Text-Fig. 15). These give off the ovular supply. Branches also arise from these ventrals and they lie in the ovary wall (Text-Fig. 15). At this stage numerous small bundles traverse the ovary wall and it is difficult to distinguish between the bundles formed by the division of the dorsal carpellary traces and the bundles derived from the ventrals. These bundles gradually fade away towards the top of the ovary (Text-Fig. 16). However, the five dorsal carpellary traces continue into the style (Text-Figs. 16–19). The ventrals after giving of the ovular supply continue into the tip of the style dividing into two each (Text-Figs. 16–20).

The ten bundles which enter the base of the cup-like structure undergo tangential splitting. First the bundles which supply the petals and antepetalous stamens undergo this splitting (Text-Fig. 17). The remaining five bundles divide a little later in the same manner (Text-Fig. 18). The bundles formed towards the inner side supply the stamens while those formed towards the outside supply the perianth members. The bundles which supply the perianth divide and form smaller bundles in the respective organs (Text-Figs. 19 and 20). Thus, the sepals, petals and stamens receive a single trace.



TEXT-FIGS. 11–20. *Garuga pinnata*. (For description see text.)

DISCUSSION

The flower in *Garuga pinnata* and *Boswelia serrata* is bisexual, hypogynous and pentamerous. However, the number of carpels in *Boswelia* is only three. Unisexual flowers also occur in the family.

The sepals in *Boswelia* and *Balsamodendron mukul* (Shukla, 1955) are 3-traced and they arise in two whorls, the sepal midribs and the conjoint sepal laterals. In *Garuga*, however, the sepals are single-traced and show adnation with the staminal traces opposite them.

The petals in the species so far investigated are single-traced. They arise independently from the main stele in *Balsamodendron mukul* (Shukla, 1955); in *Canarium nitidum* (Saunders, 1939) and *Garuga pinnata* they show adnation with the traces of the antepetalous stamens and in *Boswelia* there is adnation between the sepal laterals, petal midribs and the antepetalous staminal traces.

Boswelia and *Canarium* (Saunders, 1939) exhibit obdiplostemony. In these species the traces for the antepetalous stamens which arise conjointly with the petal midribs become demarcated earlier than the traces for the antesepalous whorl of stamens. In *Balsamodendron* (Shukla, 1955), although the traces for the stamens arise in two whorls, the antesepalous staminal traces are organised earlier than the traces for the antesepalous stamens. In *Garuga* the traces for the stamens show adnation with the midribs of the perianth members.

Boswelia and *Balsamodendron* (Shukla, 1955) resemble some species of Meliaceæ (Narayana, 1958 and 1959) and Simarubaceæ (Narayana and Sayeeduddin, 1958) in having staminal traces giving branches towards the inside.

A disc is present in all the species investigated except in *Garuga pinnata*. In *Balsamodendron* (Shukla, 1955), however, it has been interpreted as staminal in nature.

There are five carpels in *Garuga* and three in *Boswelia*. Dorsal carpellary traces are demarcated in all the investigated species. In *Boswelia* median dorsals are also demarcated at the same level where the dorsal carpellary traces are demarcated; these continue to the top of the ovary while the dorsal carpellary traces fade out early after their demarcation. The common ventrals organised from the main stele lie on the septal radii. The stylar supply in *Garuga*, *Balsamodendron* (Shukla, 1955) and *Canarium nitidum* (Saunders, 1939) consists of the dorsal carpellary traces and the common ventrals which divide into two each. In *Boswelia*, however, the style receives only the ventrals each of which divides into two.

The placentation in *Garuga pinnata* and *Boswelia serrata* is anatomically parietal (Puri, 1952) as in *Balsamodendron mukul* (Shukla, 1955) and *Canarium nitidum* (Saunders, 1939).

Summary

The floral anatomy of *Boswelia serrata* and *Garuga pinnata* has been studied.

A cup-like structure is formed by the adnation of perianth parts and stamens in *Garuga*.

The sepals are 3-traced in *Boswelia* and single-traced in *Garuga.*

The petals in both the species are single-traced and they show adna tion with the traces of the stamens opposite them.

Obdiplostemony is present only in *Boswelia.* The emerging staminal traces give branches towards the inside in *Boswelia.*

The ovary is five carpellary in *Garuga* and tricarpellary in *Boswelia.* Dorsal carpellary traces are demarcated in both the species. In *Boswelia* median dorsals are also demarcated. The stylar supply in *Garuga* consists of dorsals and ventrals while in *Boswelia* it consists of only the ventral bundles.

Placentation is anatomically parietal.

My grateful thanks are due to Prof. J. Venkateswarlu for suggesting the problem, Dr. C. V. Rao for his valuable criticism, Prof. M. Sayeeduddin for encouragement and guidance and Mr. K. V. N. Rao and Mr. N. Ramayya for the material of *Boswelia serrata.*

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ROOT ECOLOGY OF *DICHANTHIUM ANNULATUM* STAPF.

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Introduction

Grasses possess two distinct root systems. The seminal root system supports the seedling for a considerable time after seed germination while the secondary or nodal root system fixes and supplies the nutrients and water to the adult plant. The relative longevity of the seminal root and nodal roots varies from plant to plant (Troughton, 1957). Much work on ecological studies of roots of grasses of the Great Plains (Weaver and Albertson, 1956) and American prairie (Weaver, 1954) is quite a leading contribution to grassland ecology. Recently Weaver (1958) reviewed the literature on work done on underground systems of prairie plants and laid emphasis on monolith method of root sampling to study intimate relationships between root distribution and soil horizons. In a country like India, where periodic and devastating floods and droughts occur, a study of soil root relationships of vegetation is quite helpful in providing basic knowledge towards potentialities of the soil in relation to natural flora. So root ecology of *Dichanthium annulatum* was taken up for study since the species is reported as a dominant grass from the two major grassland types of India (Whyte, 1957).

Methods of Study

Soil-root monoliths of *Dichanthium* (Plate VII, Fig. 1) are collected from the sampling plot after the method described by Weaver (1958). A three-inch core type sampler with fine cutting edge and marks at 10 cm. intervals is used. The herbage of *Dichanthium annulatum* is cut off and the sampler is hammered down the rooting zone to collect soil samples at 0–10 cm., 10–20 cm., 20–30 cm., 30–40 cm. and 40–50 cm. soil horizons.

Soil Analysis

Water-holding capacity, moisture equivalent, soil reaction and water-soluble salts with conductivity meter are determined by the methods after Piper (1947). Organic matter is estimated by chromic acid digestion (Piper, 1947). Nitrogen is estimated by the method after Subbiah and Asija (1956). Ca, Mg, K and Na are leached out from the samples by barium chloride—triethanolamine at pH 8·1 (Mehlich, 1953). Ca

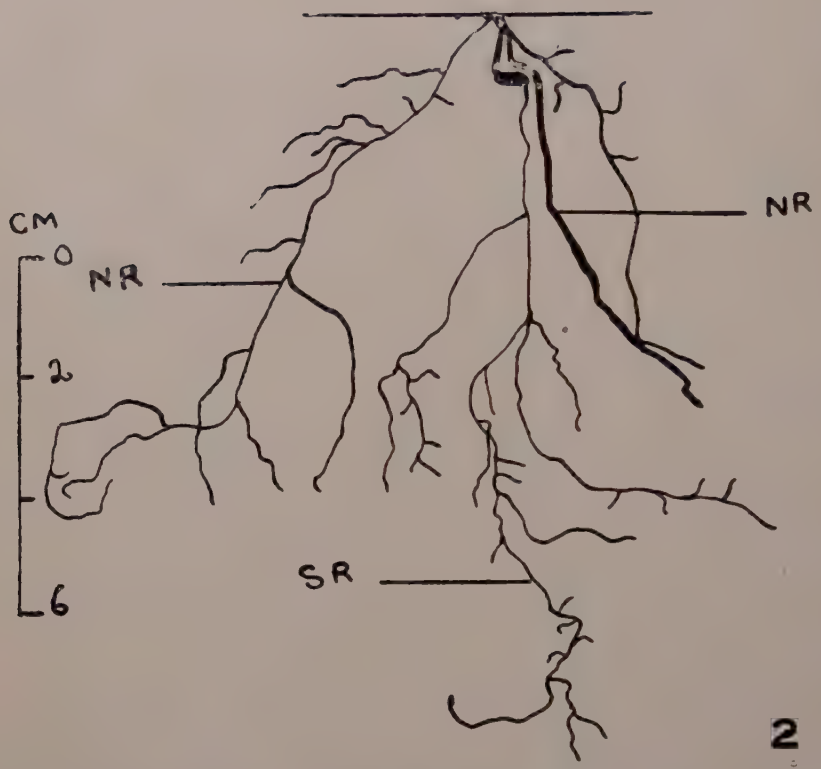
is estimated volumetrically against permanganate as oxalate; Mg is estimated colorimetrically with Beckman DU Spectrophotometer as thiazol-lake. K and Na are determined with Lang 5/56 model Flame photometer. Cation exchange capacity is determined by versenate method (Perkins, 1952).

Vegetation and Soil

Dichanthium annulatum Stapf. is a perennial, tufted and deep rooted grass being one meter tall with ascending culms, and bearing bearded and purplish nodes, from rhizomatous stem. It occurs on pale brown soils either as pure stands or mixed with populations of species of *Setaria glauca*, *Cynodon dactylon* and *Bothriochloa pertusa* in the meadows of the Banaras Hindu University grounds, where weeds like *Croton sparsiflorus*, *Crotolaria medicagenia*, *Evolvulus nummularius*, *Evolvulus alsinoides*, *Orthosiphon pallidus*, *Cassia tora*, *Scoparia dulcis* and *Indigofera linifolia* grow together during the monsoon period. Care is taken to collect soil-root monoliths and soil samples from pure stands of *Dichanthium annulatum* from sampling plots in the Botanical Garden set free from cutting and grazing. The Banaras Hindu University area is put under the western uplands bordering Ganga sand in the soil survey map of Banaras District (Agarwal and Mehrotra, 1952), and the soils are designated as Benaras type III. The surface soil colour is pale brown (10Y R 6/3; 6/2 when moist as per Munsell chart), with silty clay loam texture.

The Seminal root

A single whitish seminal root emerges out on germination of the seed of *Dichanthium annulatum*. It is about 10 cm. long and ·029 cm. in diameter, and is clothed with root hair-like structures throughout at the two leaf stage of the grass seedling. Protuberances of the first order branches appear at this stage. Remains of the pericarp persist at the 4th leaf stage. The seminal root elongates further and the first order laterals extend 6 cm. wide and the 2nd order laterals also appear at this time. The main seminal root is now about 14 cm. in length. Most of the primary laterals concentrate on the middle of the main seminal root. Nodal roots of 0·5 to 0·8 cm. length develop on the first coleoptilar node at the 4th leaf stage. At the 5th leaf stage Text-Fig. 1 the seminal root branches quite prominently and permeates the soil with larger absorptive area. More laterals arise showing frequent branching. One of the two nodal roots bears the primary laterals figuring prominently on one side of the seminal root. These lengthen up to 10 cm. and the laterals extend from 2 to 5 cm. The third unbranched stout nodal root of about 8 cm. length is also found. The seminal root persists up to the time of growth of the tillers. At later stages, it withers and gets thinned thus leaving the function or absorption and fixation of the seedling to a succession of secondary of adventitious roots. In this way the single seminal root persists up to 30 to 35 days from the time of emergence of the young seedling in *Dichanthium annulatum*.



TEXT-FIG. 1. Root system of seedling of *Dichanthium annulatum* Stapf. at 5th leaf stage.

SR = Seminal root.
NR = Nodal root.

Root Distribution

Dichanthium annulatum has an indeterminate rhizomatous stem which produces culms and secondary roots progressively. The latter penetrate quite deep into the soil. The maximum penetration of roots observed varies from 45 to 80 cm. The growth and spread of the rhizome is quite prominent and account for heavy root production in the upper 0 to 10 cm. layer of the soil. The amount of root material at this horizon ranges from 2·353 to 8·345 g. on oven-dry weight basis. The quantity of root material decreases with depth of penetration (Table I). The area of root surface exposed to soil particles is quite comparable to its deep penetration. Root surface area indices are directly proportional to the volume of the roots. The maximum value observed is '7470' with total root weight of 76·905 g. The rooting intensity index is found to vary from '2776' to '9875' (Table II). Because of prolific development of roots and rhizomes coupled with deep root

TABLE I

Root distribution of Dichanthium annulatum *Stapf.*

Soil horizons through the root zone	Number of Soil-Root monoliths studied (90 cm. × 30 cm.²)				
cm.	g	g.	g.	g.	g.
	1	2	3	4	5
0–10	2·353	2·428	3·525	8·345	5·475
10–20	1·455	1·6	2·322	6·815	7·343
20–30	0·414	0·661	1·733	4·265	3·068
30–40	0·943	0·19	0·92	2·045	0·993
40–50	..	..	0·474	0·785	..
50–60	..	..	0·172	1·23	..
Total root weight including rhizomes	21·74	20·684	31·946	37·992	76·905
Maximum rooting depth	70 cm.	52 cm.	75 cm.	45 cm.	80 cm.

penetration into the soil, *Dichanthium annulatum* serves as soil binder in soil conservation programmes.

Defoliation and Root Growth

Transplants of *Dichanthium annulatum* seedlings collected from nature were placed in wooden boxes of 90 × 30 cm.² filled with soil of silty clay loam. The grass seedlings were allowed to grow freely for 45 days. Later the herbage of the growth was clipped leaving 1 inch at the soil surface at weekly and bi-weekly intervals to simulate grazing in the field. The data are given in Table III. It is clear that the weekly clipping treatment has reduced the quantity of underground growth while bi-weekly clipping treatment encouraged tillering, new rhizome growth and root production. Hence the quantity of underground material in bi-weekly clipped plants is more than that of the control. Thus these results indicate that fortnightly grazing or cutting is advisable for profitable use of stands of *Dichanthium annulatum.*

TABLE II

Rooting intensity and root surface indices for Dichanthium annulatum *Stapf.*

Details of root study	Number of Soil-Root monoliths studied (90 cm. × 30 cm.^{2})				
	1	2	3	4	5
	cm.	cm.	cm.	cm.	cm.
Maximum shoot length	85	80	90	100	100
Maximum rooting depth	70	52	75	45	80
Root diameter ..	0·054	0·04	0·06	0·052	0·053
Diameter of rhizome (D)	0·3	0·3	0·3	0·3	0·3
Total root volume (V)	19 (c.c.)	21·5 (c.c.)	36 (c.c.)	49 (c.c.)	99 (c.c.)
Total weights of roots and stubble (W)	21·74 (g.)	20·684 (g.)	31·946 (g.)	37·992 (g.)	76·905 (g.)
Root surface index (M) (Chalyt's formula $4V/D = M$)	1407	2150	2400	3769	7471
Rooting intensity (F) $[F = (W/r^2)]$	2776	2863	3944	4906	9875

Soil Nutrients

Clay is the main source of nutrients for the growth of roots and its content is quite uniform and is high in the upper layers of the soil. The water-holding capacity is quite uniform throughout the rooting depth. Associated with heavy root production in the surface layers is the high percentage organic matter although nitrogen is quite low. Soil reaction varies from neutral point to slightly alkaline condition (Table IV).

Heavy concentration of soluble salts is noticeable in the upper layers of the soil mass. Base exchange capacity throughout the root penetration is quite uniform and ranges from 14·75 to 17·25 m.e.%. Calcium and potassium cations form the major part of the adsorption complex of the soil medium accounting for heavy root and rhizome growth and deep penetration of roots. Exchangeable sodium and

TABLE III

Defoliation frequency and quantity of underground parts of Dichanthium annulatum *Stapf.*

Treatment	No. of clippings	Rooting depth cm.	Volume of roots rhizomes c.c.	Oven-dry weights of roots and Rhizomes g.
1. Control ..	unclipped	85	70	14·5
2 *a.* Bi-weekly clipping	5	80	105	22·27
2 *b.* Bi-weekly clipping	5	82	95	23·67
3 *a.* Weekly clipping	7	72	65	10·5
3 *b.* Weekly clipping	7	77	55	10·6

TABLE IV

Physico-Chemical analysis of soil horizons through the rooting depth of Dichanthium annulatum *Stapf.*

Soil horizons through the rooting depth (cm.)	0–10	10–20	20–30	30–40	40–50
Mechanical analysis—					
Sand % ..	36·2	35·4	30–3	25	37·13
Silt % ..	20·5	36	37·5	35·5	42
Clay % ..	40	27	29	34·5	21
Water-holding capacity % ..	49·0	47·32	48·2	50·5	46
Moisture equivalent %	24·47	21·13	22·1	17·04	20·8
Organic matter % ..	1·245	1·17	0·915	1·05	1·215
Nitrogen % ..	0·034	0·018	0·039	0·036	0·029
Soil reaction ..	7·0	7·2	7·0	7·2	7·5
Water-soluble salts $\times 10^{-7}$	507·4	489·5	447·75	513·42	411·93
Exchangeable cations—					
Calcium, m.e. % ..	6·7	6·1	5·0	6·21	6·75
Magnesium, m.e. %	1·01	1·065	1·044	1·1085	1·01
Potassium, m.e. %	5·28	5·93	4·024	5·16	2·96
Sodium, m.e. %	2·112	2·288	0·968	1·408	0·281
Cation exchange capacity, m.e. %	14·75	13·25	15·7	15·0	17·25

magnesium values are quite low; Na content is 0·281 to 2·288 m.e.% and Mg cations range from 1·01 to 1·1085 m.e.%. Thus *Dichanthium annulatum* prefers heavy textured soils rich in exchangeable calcium and potassium (Table IV).

Summary

Dichanthium annulatum is described as dominant and perennial bunch grass from the meadow vegetation of the Banaras Hindu University grounds.

A single seminal root emerges from the seed of *Dichanthium annulatum* and persists for 35 days only.

Root distribution data is given for soil-root monoliths of *Dichanthium annulatum.*

Weekly clipping of the herbage of *Dichanthium annulatum* inhibits root growth both in quantity and extent.

Root zone of *Dichanthium annulatum* is rich in calcium and potassium but poor in organic matter and nitrogen content.

Acknowledgement

This paper is a part of a research project ' Soil-root relationships in grassland communities ' suggested by Prof. R. Misra, Head of the Department of Botany, Banaras Hindu University. I thank him for guidance and encouragement.

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Explanation of Plate VII

Fig. 1. Soil-root monoliths of *Dichanthium annulatum.*

FIG. 1

S. S. Ramam

BIOSYSTEMATICS OF *SISYMBRIUM IRIO* COMPLEX

IX. Genome Analysis

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(Received for publication on August 3, 1959

The first eight communications in this series (Khoshoo, 1958 *a–b*, 1959 *a–f*) deal with the genecology, morphology, cytology, synthesis, floral biology, hybridization and isolation of the various members of this complex. Keeping in view some of these data, an attempt has been made in the present paper to work out the genomic constitution of the various races within this complex.

According to the classical and conventional genome-concept, the formation of bivalents, in a hybrid between an allotetraploid and one of its putative diploid ancestors, indicates close similarity of their genomes. This, however, is only partly correct now, because, the chromosomes forming bivalents may be perfectly homologous, or may be homeologous (Stebbins, 1947, 1950; Lilienfeld, 1951; Sears, 1952; Sachs, 1953; Riley and Chapman, 1958; Riley *et al.*, 1958; Sears and Okamoto, 1958), or even the non-homologous parts of chromosomes may pair (McClintock, 1933). Therefore, the chromosomes that pair, may not be necessarily strictly identical in their structure, and in gene content and arrangement. Experience has shown that the only way to be certain about the genomic constitution of a given polyploid is to synthesize it, if the putative parents can be located; till then, all genomic formulæ are to be treated as tentative in character. If this be the guiding principle, then in the present complex, we can be sure about the constitution of the hexaploid and the octoploid, because, these races have not only been synthesized, but have also been compared and crossed with their natural counterparts (Khoshoo, 1959 *b*, *d*). On the other hand, the constitution of the tetraploid race can be deduced rather indirectly.

Before proceeding further, it is pertinent to recapitulate the chromosome associations in the various races and hybrids of this complex. A resume of this data at diakinesis, prepared from the earlier papers of the writer (Khoshoo, 1955, 1957 *b*, 1959 *a-b*, *d*), is given in Table I and would be helpful in understanding the following arguments.

Nature of the Tetraploid Race

The diploid and the tetraploid races show rigidly bivalent formation (Khoshoo, 1955, 1957 *b*, 1959 *a*). This point is rather important,

TABLE I

Name	Most common associations in a cell			Average associations per cell			
	IV	II	I	IV	III	II	I
DIPLOID ($2n = 14$)	..	7	..	..	..	7	..
COLCHI-AUTOTETRAPLOID	7	..	..	6·65	..	0·7	..
TETRAPLOID	..	14	..	..	..	14	..
HEXAPLOID							
Spontaneous	..	21	..	0·51	..	19·98	..
Artificial	..	21	..	0·7	..	19·6	..
OCTOPLOID							
Spontaneous ..	12–1	4–26	..	6·70	..	14·60	..
Artificial	13–5	2–18	..	9·64	0·12	8·00	1·08
POLYHAPLOID (of Tetraploid)	..	..	14	..	..	0·4	13·2
TRIPLOID (Diploid × Tetraploid)	7	7	..	0·02	6·79	7·36	
HYBRID-TETRAPLOID (Autotetraploid × Tetraploid)	7	14	..	0·2	6·6	14·2	

particularly as regards the tetraploid race, because it is generally believed that polyploids with small chromosomes (as is the case here) tend to form bivalents. This tendency is due to the small size of their chromosomes, which results in low chiasmata frequency due to the phenomenon of interference. As such, the possibility of the present tetraploid race being autotetraploid in character, cannot be ruled out at this stage. That it is not so, will be clear by considering the nature of pairing in the autotetraploid plants of this complex (Khoshoo, 1959 *a*). These plants were raised by colchicine-treatment of the diploid race, and showed almost complete quadrivalent formation; the average number at diakinesis being 6·65 per cell. Evidently, the bivalent formation in the tetraploid race does not appear to be due to the low chiasmata frequency as the direct result of the small size of its chromosomes. On the other hand, it appears to be purely due to the

non-homology between its two genomes, since the autotetraploid, with practically the same size and number of the chromosomes shows preponderant quadrivalent formation. Obviously, it looks reasonably certain that the tetraploid is an allotetraploid and is a perfect bivalent-former.

The second proof for the above conclusion, is afforded by the nature of the pairing in one polyhaploid individual of the tetraploid race (Khoshoo, 1957 *b*). The mean number of bivalents at metaphase I in this plant was 0·4 per cell. This small amount of pairing does not appear to be due to any strong or extensive homology, because, if it were so, there would have been corresponding frequency of the quadrivalents in the tetraploid race. On the other hand, a study of over 2,000 pollen mother-cells of the tetraploid race did not reveal any quadrivalents (Khoshoo, 1957 *b*, 1959 *a*). The low pairing in the polyhaploid could be explained as being due to the fusion of heterochromatic ends as has been clearly brought out by Kostoff (1938) in haploid einkorn wheat and by Levan (1942, 1945) in haploids of rye and sugar-beet. Heterochromatin being inert does not change and thus is expected to retain the original homology. This would result in attraction at such points particularly when there is no special attraction in euchromatin (*cf.*, Sharma, 1955). Alternatively, this pairing may indicate homology of small segments, which may be strong enough to affect pairing especially when there is a general lack of competition for pairing among the chromosomes. However, in the tetraploid race, due to the presence of completely homologous chromosomes, the little homeologous pairing is inhibited in preference to the homologous one.

From the above consideration, it is clear that there exists very little homology between the two genomes of the tetraploid race and that the sterility is only chromosomal (Khoshoo, 1957 *b*). Evidently, biosystematic relationship between the two parents of the tetraploid race is at cenospecific level. In short the tetraploid race is allotetraploid in nature. Alternatively, the two genomes involved may be homeologous and pairing between them being completely restricted due to some form of genotypic control (*cf.* Riley and Chapman, 1958; Sears and Okamoto, 1958). At present it is indeed difficult to decide once for all in favour of any one of these possibilities; however, one point is clear that the tetraploid race shows virtually no pairing between the two genomes and is at present an obligate bivalent-former. As indicated above, it has all the characteristics of a typical genomic allotetraploid (*cf.* Clausen *et al.*, 1945; Stebbins, 1947, 1950).

The morphological and ecological differentiation within the tetraploid race (Khoshoo, 1957 *a*, 1958 *a–b*) appears to be entirely at the genic level, because the hybrids within this race are perfectly fertile (Khoshoo, 1959 *d*). However, the exact nature of this genic differentiation is being studied.

Relationship Between the Diploid and the Tetraploid

The course of meiosis in the triploid (diploid × tetraploid) (Khoshoo, 1959 *a*) clarifies this relationship. At diakinesis, in 70% of the cells

of this hybrid, there is observed the *Drosera* scheme, *i.e.*, 7 bivalents + 7 univalents. That the 7 bivalents of the hybrid are due to the pairing of the chromosomes of only the tetraploid parent, can be convincingly ruled out, since there are neither any quadrivalents in the latter, nor there were noted the corresponding number of bivalents in the polyhaploid individual (Khoshoo, 1957 *b*). The only logical explanation is that the bivalents in the triploid are due to the association of 7 chromosomes of the diploid and only 7 (out of the 14) of the tetraploid. The other 7 chromosomes of the tetraploid parent, appear to be largely non-homologous and remain, therefore, generally unpaired.

If the constitution of the diploid is represented by AA, where A denotes a set of 7 chromosomes, then the autotetraploid would have AAAA constitution. The tetraploid would have AA BB constitution, where B denotes another set of 7 chromosomes, which appears to be largely non-homologous with A. The triploid hybrid would have AA B. On this basis, the occurrence of generally 14 univalents in the polyhaploid plant and of 7 bivalents + 7 univalents in the triploid hybrid, is easily explained. Furthermore, this scheme also reveals the genomic alloploid nature of the tetraploid race concluded earlier.

The above interpretation explains the associations of 7 bivalents + 7 univalents observed in 70% cells at diakinesis in the triploid. It could also explain the situation in another 16% cells (*cf.*, Khoshoo, 1959 *a*, Table II), because, these cells always had less than 7 bivalents. One may argue that in such cases the chromosomes did not get a chance to realize the full associations (*i.e.*, 7 bivalents + 7 univalents). The remaining 14% cells at diakinesis contain either more than 7 bivalents (8 or 9), or in occasional cells there were found trivalents also, though the latter were altogether absent at metaphase-I. If the extra associations in these 14% cells of the triploid are due to any strong homology, then these should have resulted in more than 7 quadrivalents (and also in some cases in hexavalents) in the hexaploid race. To recapitulate, the hexaploid is the result of gametic doubling of the triploid (Khoshoo, 1959 *b*), and in the natural hexaploid, firstly, never higher than quadrivalent associations are encountered, and, secondly, their number never exceeds two (Khoshoo, 1959 *a*). This clearly indicates that the increased pairing (*i.e.*, associations more than 7 bivalents + 7 univalents), in triploid is not due to any extensive homology. The mean number of quadrivalents per cell in the natural hexaploid race is 0·51 at diakinesis, and 0·7 in artificial hexaploid individuals at the same stage (Khoshoo, 1959 *a*, *b*). Furthermore, these quadrivalents are only loosely associated (Khoshoo, 1959 *a*, Figs. 35, 37). Two important conclusions can be drawn from the above observations.

Firstly, the occurrence of more than 7 bivalents (8 or 9) and also occasional formation of a trivalent, reveal that homologous segments are distributed even among A and B genomes. Earlier, a similar conclusion was also hinted at, while discussing the pairing of the polyhaploid. The alternate reason for the increased pairing in the triploid and also of the polyhaploid, may be the fusion of heterochromatic regions.

Secondly, even the 7 bivalents of the triploid are not entirely homologous in character. Had these been so, one would encounter much higher quadrivalent frequency in the hexaploids than is actually seen. This indicates that the chromosomes forming the bivalents show cryptic structural hybridity, or are only homeologous. Such chromosome would easily pair in the triploid, especially when there is a lack of competition for pairing. This is further supported by the fact that the bivalents in the triploid are often loosely attached at diakinesis, and at metaphase-I these are long and attenuated (Khoshoo, 1959 *a*). At any rate, these are never as much contracted as the bivalents of all the other races. Furthermore, at anaphase-I, the bivalents of the triploid form bridges with and without fragments, implying thereby that the pairing chromosomes differ by inversions (Khoshoo, 1959 *a*). All these facts when taken together, strongly point towards the differentiation of the chromosomes that organise bivalents in the triploid, *i.e.*, they are not completely homologous. It may be concluded that in the triploid, homeologous chromosomes pair; while, on duplication (*i.e.*, in hexaploid) their pairing is suppressed, due to the preferential pairing between the homologous chromosomes. Obviously, the above discussion reveals that the genomic constitution of the triploid is not AA B, as concluded earlier, but there is strong evidence for its being something like AA_1 B, where A_1 is a homeologous or a partially homologous set of chromosomes. Furthermore, there is some segmental homology even between the chromosomes of A and A_1, with those of the B genome; this would account for the pairing in polyhaploid and the increased pairing (more than 7 bivalents) in the triploid. If we denote the constitution of the diploid as AA, then the tetraploid race has a constitution like A_1A_1 BB, instead of AA BB as concluded earlier.

Further proof to the above analysis comes from the nature of pairing in the hybrid-tetraploid (autotetraploid $\times$ tetraploid) (Khoshoo, 1959 *d*). If the A genomes of the diploid and the tetraploid are extensively homologous, then one could reasonably expect to have 7 trivalents + 7 univalents in the hybrid-tetraploid; at any rate the frequency of trivalents would be much higher than 0·2 per cell. It is pertinent to point out here that Howard and Manton (1946) have seen a high frequency of trivalents in a similar hybrid-tetraploid in *Nasturtium officinale* complex. On the contrary, in the present hybrid-tetraploid we find generally 7 bivalents + 14 univalents. The average number of bivalents per cell being 6·6, that of univalents was 14·2 and of the trivalents only 0·2 per cell (Khoshoo, 1959 *d*). Furthermore, the bivalents are always of the closed type and there were none of the open type seen in the triploid (Khoshoo, 1959 *a*). Evidently the 14 chromosomes forming the 7 bivalents are identical and are the ones that were contributed by the autotetraploid parent. The remaining 14 chromosomes that generally remain unpaired, belong obviously to the tetraploid race. These chromosomes generally also remained unpaired in the polyhaploid. The association of 7 bivalents + 14 univalents in the hybrid-tetraploid can be easily explained if we regard its genomic formula as, AA A_1B [autotetraploid (4 A) $\times$ tetraploid (2 A_1 2 B)], and not AAA B,

as expected in case we regard the A genomes of the diploid and the tetraploid as perfectly identical.

One more evidence may now be considered in favour of the above conclusion. For this, a comparison of the triploid hybrid of the present complex with that of a similar hybrid in *Nasturtium officinale* complex (Howard and Manton, 1946) is pertinent. In the latter, the bivalents are formed due to the homology of the A genome of the diploid parent with the A genome of the tetraploid parent. As such at meiosis each spore is expected to get at least one harmonious set of chromosomes. The only cause of reduced fertility is the unequal segregation of the univalents. This is corroborated by the fact that the triploid hybrid in *Nasturtium* leaves some progeny, and as expected, it is aneuploid (*cf.*, Howard and Manton, 1946). On the other hand, the total sterility (barring some rare hexaploid seeds) in the triploid of *Sisymbrium* (Khoshoo, 1955, 1958 *b*, 1959 *a*, *b*), can be explained because of the partial homology of the chromosomes that form the bivalents in it. It is reasonable to expect that the spores would get disharmonious sets of chromosomes due to the recombination of the partially homologous chromosomes. Furthermore, the unequal segregation of the univalents would augment the inviability of the spores. On this reasoning, it is easy to explain the partial sterility in the triploid *N. officinale*, while the total sterility in the present triploid. Therefore, it gives an added, but an indirect, evidence in favour of the differentiation of A genomes of the diploid and the tetraploid races.

The above discussion reveals that one of the pivotal points, on which the conclusion about the differentiation of A genomes in the diploid and the tetraploid is based, is the presence of an extremely low quadrivalent frequency in the natural hexaploid than is expected on the basis of the bivalent formation in the triploid. In this connection, one more argument has to be examined. The absence of the expected number of quadrivalents in the hexaploid may be due to a "special genotypically controlled tendency to bivalent formation" as advocated by Müntzing and Prakken (1940) and Nordenskiöld (1941) for a similar lack of quadrivalents in *Phleum pratense*. Recently experimental support for this theoretical suggestion has come from the work on wheat (Riley and Chapman, 1958; Sears and Okamoto, 1958). It has been shown that a genotypic basis is at work in the hexaploid wheat, which is normally an obligate bivalent-former and a species in which such a mechanism was hardly suspected. In view of these findings the present writer does not outright exclude the possibility of such a basis, working for the predominant bivalent formation in the hexaploid and, in particular, in the tetraploid of the *S. irio* complex. However, from the evidence gathered so far, bivalent formation in these races and also in the hybrid-tetraploid appears to be more a question of homology of their genomes in the manner suggested above. On the other hand, the autotetraploid and the octoploid commonly form quadrivalents because each chromosome is represented four times.

Finally, the conclusion about the differentiation of the A genomes of the diploid and the tetraplid, poses the question, as to whether the present diploid is one of the two parents of the tetraploid! At present, both the possibilities may be considered. One of these is that, keeping in view the above conclusion, the present diploid has not been the exact source of the A genome of the tetraploid, it may very well have come from a close relative (A_1A_1) of the diploid race. However, on the morphological grounds, it may be pointed out that the present diploid does fit fairly well as one of the parents of the tetraploid race. Therefore, it is not unlikely that since the time A genome has entered in association with the B genome (to form the present tetraploid), both these genomes have undergone some degrees of structural rearrangement and genetical divergence, as compared to the original condition. The wide distribution of the tetraploid race (unpublished data), indicates that it is quite an old taxon and ever since its origin many changes may have occurred in its genomes. If this is correct then the original A genome is present in the diploid, which shows no apparent differentiation between its European and Indian populations. Furthermore, when the original and the differentiated A genomes are brought together in the triploid, the two do not recombine harmoniously. The B genome is so far not traceable, but once it is identified, it is not unlikely that it would also show a similar differentiation. It may be concluded that the final proof about the exact relationship between the present diploid (AA) and the tetraploid race would be forthcoming only when the latter has been synthesized.

Nature of the Hexaploid and the Octoploid

Earlier, the present writer (Khoshoo, 1959 *b*) has conclusively shown that the hexaploid race is an amphiploid between the diploid race and the tetraploid *caulis* type. It has arisen through the gametic doubling of the natural triploid hybrid. If we denote the genomic constitution of the diploid as AA, then that of the tetraploid would be A_1A_1 BB. The constitution of the hexaploid race would therefore be AA A_1A_1 BB. This race is an auto-allohexaploid, whose autoploid portion (AA A_1A_1) is in itself segmental-alloploid in character.

The natural octoploid plants were demonstrated to be autoploid derivatives from the tetraploid race and have arisen from its ' off season ' plants. Due to the summer heat ' modificative asynapsis ' occurs in such plants and unreduced spores are produced which on fertilization give rise to the octoploid individuals (Khoshoo, 1959 *b*). The genomic constitution of the octoploid plants is, therefore, easy to infer, and is $4A_1$ 4B. They are auto-allo-octoploid in character.

The artificial hexaploid shows a little higher (0·7 per cell) quadrivalent frequency than its natural counterpart (0·51 per cell) (Khoshoo, 1959 *a*, *b*). This is also true of the artificial and the natural octoploids. At diakinesis, the former has 9·64 quadrivalents per cell, while in the latter there are only 6·70 per cell (Khoshoo, 1959 *a*, *b*). This increase in the quadrivalent frequency in the artificial entities is due to the fact

that these are raw and are likely to contain more duplicated material. In nature there would take place a selection for the elimination of quadrivalents, because of the progressive diploidization. This could be achieved either by elimination of the duplicated regions, or by rendering such regions non-homologous by fixation of new gene mutations. Perfect diploidization could also be brought about in a much shorter time by fixation of specific mutations for bivalent formation. This would outright suppress all homeologous pairing as seems to have happened in hexaploid wheat (Riley and Chapman, 1958; Sears and Okamoto, 1958).

It is pertinent to point out here that there is evidence for rearrangement in the chromosomes of the raw and the natural hexaploids and octoploids (Khoshoo, 1959 *d*). The hybrids between natural and the artificial entities show bridges with and without fragments. This rearrangement seems to have occurred without any corresponding change in the morphology of the plants. It is not unlikely that the occurrence of the repatterning in the chromosomes of both the natural hexaploid and the octoploid races, may very well be due to the difference in the original strains involved in evolution of the natural races and those utilized by the present writer for the production of their artificial counterparts. Such inter-liner or inter-biotypic differences within the diploid and the tetraploid races have yet to be unravelled. There appears another very important reason for this difference and it relates to the mode of their origin. In nature these races arise by gametic doubling, while their synthetic counterparts were produced by somatic doubling (Khoshoo, 1959 *b*).

The foregoing analysis has been summarized in Fig. 1.

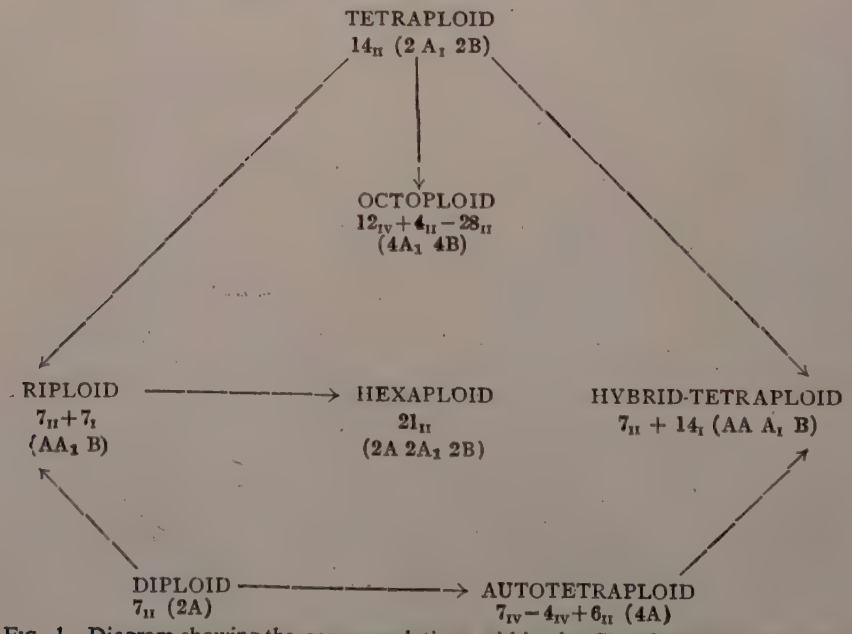

FIG. 1. Diagram showing the genome-relations within the *Sisymbrium irio* complex.

Conclusions

The various evidences point out that if the genomic constitution of the diploid race is denoted as AA, then that of the tetraploid is 2 A_1 2 B. The hexaploid has a constitution like 2A 2A_1 2B, while the octoploid has 4A_1 4B. Following the nomenclature of Stebbins (1947, 1950), the tetraploid is a genomic allotetraploid. The hexaploid is an auto-allohexaploid, whose autoploid portion is in itself segmental-alloploid in character. The octoploid is an auto-allo-octoploid.

The pairing in the polyhaploid (Khoshoo, 1957 *b*) plant and the increased pairing (*i.e.*, more than 7 bivalents and/or occasional trivalent formation) in the triploid (Khoshoo, 1959 *a*), indicate that the A and A_1 genomes on one hand, and the B genome on the other, are not entirely non-homologous. Furthermore, some duplicated segments appear to be randomly distributed among the chromosomes of the A genomes and the B genome. Ordinarily such homeologous associations are suppressed, either due to the strong preferential pairing or due to some, hitherto unravelled, genotypic control. This means that the symbols A, A_1 and B do not convey the real cytogenetical nature of the genomes.

The taxonomic implications of the present analysis will be published elsewhere in due course.

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A CONTRIBUTION TO OUR KNOWLEDGE OF THE VEGETATION AND FLORA OF THE PACHMARHI PLATEAU AND THE ADJACENT REGIONS*

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Introduction

The Pachmarhi plateau and parts of the neighbouring hilly tracts, namely, the Satpura and the Mahadeo hills of the parts of Chindwara, Betul and Khandwa forest divisions of the Madhya Pradesh are botanically little known parts of India (Map 1). There is no complete published record of the entire flora of this region similar to the floras of Madras, Bombay, Bihar and Orissa and Bengal and as such any published account of the botanical collections of these areas can only be a welcome addition to our knowledge of the vegetation of these regions.

The first published account of the forests and the natural history of this region is by Capt. James Forsyth in his book on "The Highlands of Central India," in 1872 (Second Edition). Subsequently, publication by Brandis and Stewart (1874), chiefly concerning the arboreal vegetation of a small part of the area, Gamble (1892) about a few ferns collected by Duthie in 1891, Hole (1906) dealing with forest areas other than the Pachmarhi plateau, Witt (1908, 1911, 1916) regarding forest vegetation of the Berar Circle and adjacent regions, Graham (1914–15) about the ferns from the ravines and gorges of the Pachmarhi plateau, Mukherjee (1923) whose paper dealing with plant association from the open flat country near Piparia to the top of the Pachmarhi plateau was not published and Pandé and Srivastava (1952) regarding Hepatic flora of the Plateau, are the only additional contributions to the Botanical knowledge of the area under study.

Geology, Soil and Climate

Different types of Geological formations are represented in this area but the main type is Gondwana formation chiefly composed of

The work was carried out at the Calcutta Herbarium when the senior author was attached to it.

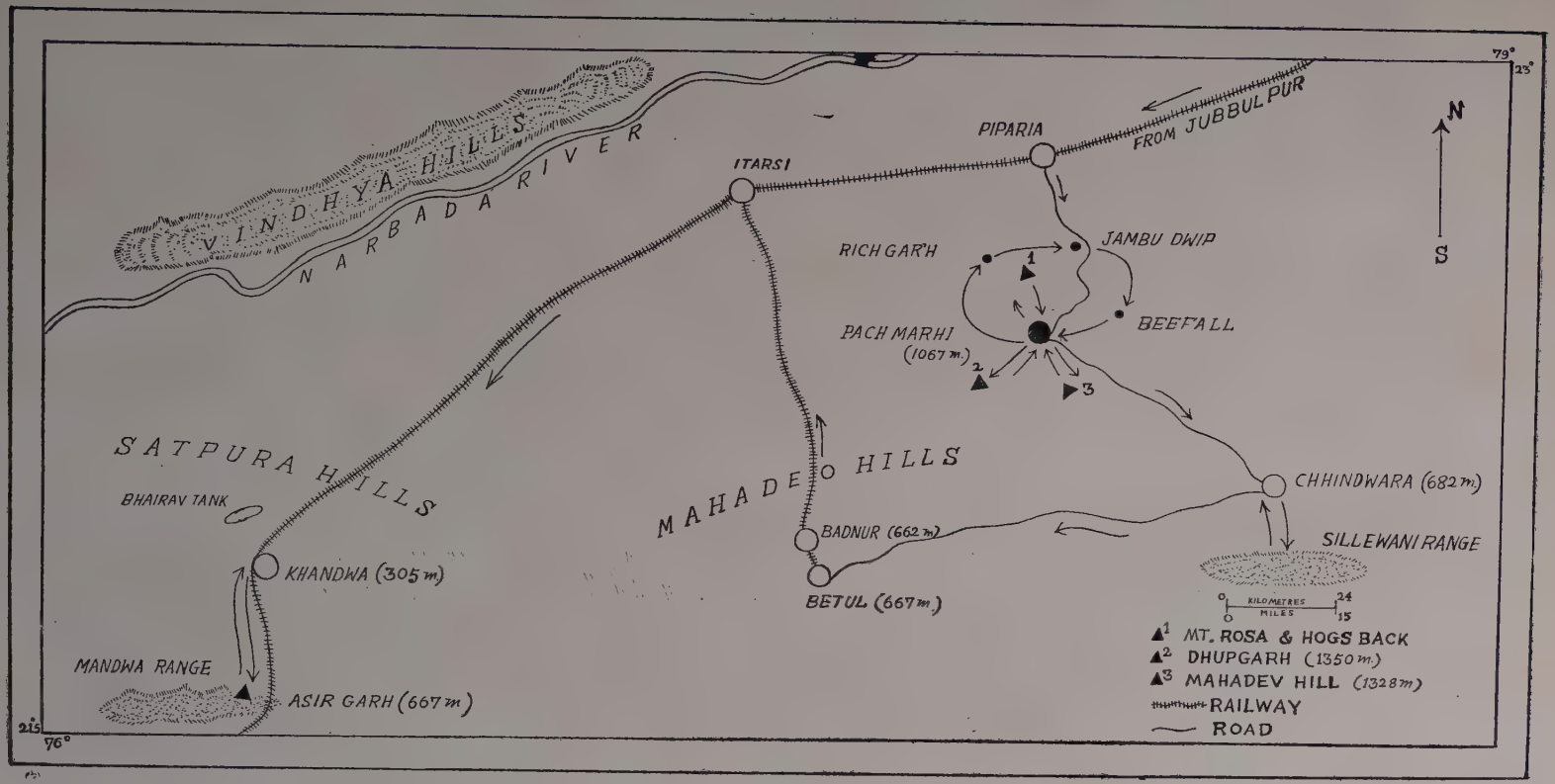
sandstones and shales. In the Pachmarhi hills, these rocks consist chiefly of coarse sandstones and conglomerates. The southern part of the Betul and the Nimar divisions (Khandwa) show the Deccan trap formation with the basaltic rocks. The undulating plain around Betul is covered by fertile black cotton soil. The climate is comparatively cooler than the northern districts of the Vindhya Plateau with 40° C. as the average maximum and 22° C. as the average minimum temperature in summer and 8° C. as the average minimum in winter and with an average rainfall of 125–200 cm.

Vegetational Account

The vegetation of this area is typically of a dry deciduous type. The components of the vegetation are characteristically similar to those found in the dry deciduous forests of the Santal Parganas in Bihar and of the Eastern Ghats in Orissa and Andhra regions. On the basis of the collections made in this area by the party of the Botanical Survey of India and a few other collectors, the families, Gramineæ, Papilionaceæ, Euphorbiaceæ, Cyperaceæ, Acanthaceæ, Compositæ, Verbenaceæ, and Malvaceæ, are more or less well represented. Considerable change has been observed in the main component of the vegetation of the different zones of the area. *Shorea robusta*, the 'Sal' which is particularly common on sandstone, conglomerate and gravelly soils, is dominant around Pachmarhi and Mahadeo hills, constituting almost pure consociation in certain areas. But the trees are stunted, weak-stemmed and badly damaged by insect-borer. Beyond Chindwara and towards Betul, *Tectona grandis*, the 'Teak' is fairly common, growing on trap as well as sandstone. In general, the plants on the drier soil show a poorer growth in comparison to those growing on well-drained slopes and in the valleys where the soil is covered with rich deep loam. On the western side towards Asirgarh on the Mandwa range, *Boswellia serrata*, the 'Salai' and *Hardwickia binata*, the "Anjan" are the dominant species, forming in certain spots, what may be called pure groups, on the dry trap hills.

In view of the above components of the vegetation, the area under study can be divided into three well-marked zones, namely, (1) Pachmarhi Zone, (2) Chindwara-Betul Zone and (3) Khandwa-Asirgarh Zone.

(1) *Pachmarhi Zone.*—The road from Piparia to Pachmarhi is lined on either side for a distance of about fourteen miles with more or less uniform vegetation consisting of *Hardwickia binata*, *Terminalia tomentosa*, *Anogeissus pendula*, *Acacia*, *Albizzia* and others. The undergrowth is composed mainly of *Tephrosia*, *Justicia*, *Rhus parviflora*, and various grasses like *Digitaria*, *Panicum*, *Eragrostis* and others. As the plain is gradually crossed, reaching an elevation of 610 m. (= 2,000 ft.), the character of the vegetation begins to change. The open dry vegetation with sparse growth of trees of the lower region is gradually replaced by dense green vegetation thickly covering the soil.



MAP 1. Showing the various regions explored. Arrows indicate the route followed along the regions.

Pachmarhi, a corruption of 'Panch Mathi' or five huts, is a plateau of about 60 sq. kilometres (= 23 square miles) at an elevation of 1,067 m. (= 3,500 ft.), surrounded by prominent peaks like Mahadeo (1,328 m. =4,358 ft.) on the south, Chauradeo (1,312 m.= 4,303 ft.) on the south-east and Duphgarh (1,350 m. = 4,429 ft.) on the south-west. The remarkable feature in the configuration of the plateau is the vast and unexpected ravines or rather clefts in the solid rock which seam the edges of the scarp, some of them reaching in sheer descent almost to the level of the plains. Such areas, which are usually under the constant influence of flowing water, are devoid of vegetation, presenting barren, rugged appearance. At certain places the moist banks of streams are covered with liverworts, mosses and ferns like *Adiantum philippense*, *Gleichenia linearis*, *Osmunda regalis* and others. In moist ravines, tree ferns like *Cyathea gigantea* and *C. latebrosa* add to the grace of the surroundings. The data collected during the study of the various regions, placed in and around Pachmarhi like Richgarh, Mount Rosa, Hogsback, Jambu Dwip and Bee Fall, indicate that the vegetation in general is quite uniform with *Shorea robusta* as the dominant species mixed with *Terminalia tomentosa*, *T. chebula*, *Lagerstræmia parviflora*, *Sterculia villosa*, *Dillenia pentagyna*, *Gardenia turgida*, *Manilkara hexandra*, *Buchanania lanzan*, *Careya arborea*, *Garuga pinnata* and others. The undergrowth includes characteristic shrubs like *Grewia*, *Carvia*, *Helicteres*, *Moghania*, *Combretum*, *Phyllanthus* and the bamboos, *Dendrocalamus* and *Bambusa* and a palm, *Phœnix humilis*. The ground cover is occupied by herbs like *Cissampelos*, *Sida*, *Triumfetta*, *Crotalaria*, *Desmodium*, *Indigofera*, *Alysicarpus*, *Tephrosia*, *Melastoma*, *Ageratum*, *Vernonia*, *Trichodesma*, *Ipomœa*, *Justicia*, *Leucas*, *Gomphrena*, *Achyranthes*, *Euphorbia*, *Acalypha*, *Commelina*, *Eriocaulon* and a large number of sedges and grasses. The common climbers round about the plateau are *Bauhinia vahlii*, *Cissus*, *Argyreia*, *Ipomœa*, *Smilax*, *Dioscorea*, *Gloriosa* and *Asparagus*. There are also a few parasites like *Dendrophthœ*, *Scurrula*, *Viscum*, *Cassytha* and *Cuscuta*. Interestingly enough, epiphytic orchids with the record of only one species, *Vanda parviflora*, appears to be rather rare and a few terrestrial orchids like *Habenaria* with a good number of species, *Microstylis*, *Peristylus*, *Goodyera* and *Geodorum* have been collected. Some of the interesting collections near the watery edges and other moist places are *Ophioglossum* and *Equisetum debile* mixed with other ferns like the different species of *Cheilanthes*, *Abacopteris*, *Tectaria*, *Blechnum*, *Sphenomeris* and *Pteris* and with herbaceous angiosperms like *Justicia*, *Impatiens*, *Kickxia* and *Lindernia*. On a shady moist hill slope covered by *Shorea robusta*, a luxuriant growth of *Gleichenia linearis* mixed partly with *Melastoma malabathricum*, has been observed. At certain water-logged parts of the plateau, a swampy area is formed where a carnivorous plant, *Utricularia wallichiana* and members of Cyperaceæ like *Cyperus*, *Scirpus*, *Fimbristylis* and other plants like *Eriocaulon*, *Commelina*, *Cyanotis*, *Oxalis*, *Eclipta*, *Justicia*, *Alternanthera*, *Achyranthes* and grasses such as *Eragrostis*, *Ischæmum* and *Panicum* were collected. A very showy grass, *Rhynchelytrum villosum* with its violet-coloured inflorescences has been found to be quite common on the plateau. On

certain slopes where the rocks are steep, barren and eroded, huge plants of *Euphorbia neriifolia* and *E. nivulia* form the dominant vegetation. In some dry corners, an interesting species, *Selaginella bryopteris* with its recurved leaves has been collected. At certain places the soil erosion is so prominent that actually a large quantity of sand, wholly destitute of any vegetation, was found accumulated at the foot of Mount Rosa by the constant action of water on sandstone. The interesting new records of the Pachmarhi plateau and the adjacent hills are the occurrence of the Himalayan species, such as, *Thalictrum foliolosum* (Hog's back) and *Chirita bifolia* (Pachmarhi).

On the way to Dhupgarh from Pachmarhi the altitude varies from 1,067 m. (= 3,500 ft.) to 1,311 m. (= 4,300 ft.) and the vegetation comprises of *Shorea robusta*, a dominant species mixed with *Gardenia turgida*, *Sterculia*, *Salmalia* and *Albizzia* with the undergrowth of plants like *Sida*, *Triumfetta*, *Carvia*, *Phyllanthus*, *Helinus*, *Curculigo* and grasses like *Thysanolæna* and *Apluda*. Climbers like *Schefflera*, *Dioscorea*, *Gymnema sylvestre* and *Naravelia zeylanica* are common. *Habenaria* appears to be the common terrestrial orchid in this area. In some of moist corners and crevices, plants like *Marchantia*, *Funaria*, *Begonia* and a few members of Scrophulariaceæ already mentioned, have been collected. In some of the water-logged areas *Utricularia wallichiana* and *Lemna* have been noted. Some of the interesting plants which have not been so far recorded from this area are *Ceropegia macrantha*, a temperate Himalayan plant, the two aroids, *Plasmonium margaritiferum* and *Remusatia vivipara*, a subtropical Himalayan aroid, members of Umbelliferæ like *Bupleurum* and *Pimpinella*. Other records are noted in the enumerated list given at the end. The two essential oil-yielding plants, *Jasminum grandiflorum*, 'the Chameli' and *Micromeria biflora*, have been observed for the first time, growing quite abundantly as an undergrowth on the Duphgarh hill-top.

The way to Mahadeo hill and the neighbouring valleys lies through open woodland, primarily consisting of *Shorea robusta* (Sal) mixed with *Terminalia* species, *Buchanania lanzan* and *Ougeinia oojeinensis*. *Hardwickia binata* and *Adina cordifolia* have also been observed here and there on the lower slopes. The undergrowth consists of various plants like *Acanthospermum*, *Emilia*, *Celosia*, *Moghania*, *Desmodium*, *Cynoglossum*, *Bæhmeria* and only a few grasses such as *Panicum*, *Paspalum*, *Eragrostis* and *Dendrocalamus*. However, "Rusa grass" (*Cymbopogon martini*) appears to be the most common species in this area. The highly shady rocky surfaces are, as usual, covered by *Marchantia*, *Funaria*, *Pyrrosia*, *Pteris*, *Athyrium* and such other moisture-loving plants. The interesting observation made at the foot of the Mahadeo hill is the Mahadeo cave which opens itself through a lofty natural arch in a vertical sandstone cliff and runs straight into the bowels of the hill for about 91 m. (= 300 ft.) and a stream of clear cold water comes from a cleft at the further end of the cave. Due to the constant action of water, a perfect sandy layer is formed near the mouth of the cave where plants characteristic of sandy shore, like *Zornia diphylla*, *Borreria hispida* and *B. stricta*, have been collected.

(2) *Chindwara-Betul Zone.*—The vegetation on the way to Chindwara and Sellewani range (610 m. = 2,000 ft.) is practically dominated by *Tectona grandis*, "the Teak" which shows poor growth, except on fertile well-drained slopes and valleys. Along with Teak, the common trees are *Ougeinia oojeinensis* and *Lannea grandis*, *Terminalia tomentosa* and *Anogeissus latifolia*, forming mixed association. In certain tracts, *Dendrocalamus strictus* is rather very common, covering the undergrowth of the mixed Teak forest. Other trees like *Pterocarpus marsupium*, *Diospyros melanoxylon*, *Lagerstræmia parviflora*, *Adina cordifolia* and a few others have also been noted along with Teak, forming dense forest. The shrubby and the herbaceous growth are composed of mostly the common species as already reported, without much variety. But, some of the interesting plants which have been collected from this area are *Ceropegia hirsuta*, *Hibiscus lobatus*, *Aristida*, one of the common grasses of the area and *Nyctanthes arbor-tristis* with fragrant flowers, frequently gregarious forming dense thickets. Climbers like *Bauhinia vahlii*, *Ampelocissus tomentosa*, *Millettia*, *Butea* and *Ipomæa* and terrestrial orchids like *Habenaria platyphylla* have also been observed.

The Betul area may be described as a Central Plateau surrounded by a belt of hilly and forest-covered country. Excepting the northern sandy stone part of the Betul area where Sal forms the dominant component of the vegetation, the vegetation of the remaining parts shows the dominance of Teak mixed with *Ougeinia*, *Anogeissus* and the other common species already mentioned above. The plain around Betul, which consists of a fertile Black-cotton soil, consists of common trees like *Terminalia*, *Syzygium* and here and there *Boswellia* apart from the usual forest trees. In general, grasses and members of Leguminosæ appear to be very common in the Chindwara-Betul Zone.

(3) *Khandwa-Asirgarh Zone.*—This zone which includes a large plain at about 305 m. (= 1,000 ft.) elevation with a few peaks like Asirgarh (667 m. = 2,189 ft.), rising conspicuously and with the Deccan-trap formation, exhibit a characteristic vegetation mainly composed of *Boswellia serrata*, the "Salai" and *Hardwickia binata*, the "Anjan". A few species of *Gmelina*, *Sterculia* and *Acacia* are also associated with the main components. At certain places on the way from Khandwa to Asirgarh, somewhat pure groups of either *Boswellia* or *Hardwickia* have also been observed. The undergrowth is mostly occupied by large number of grasses, of which *Aristida* and *Apluda* are very common. The climbers are comparatively few and only a few species like *Cayratia* and *Abrus* were noted. Interestingly enough, on the hill slopes around the Fort of Asirgarh, "Russa grass", *Cymbopogon martini* has been observed, growing quite abundantly. Further, the "False Bhabar", *Eriophorum comosum*, a tufted sedge with wiry stems and long leaves which has been spoken of as excellent as "Esparto grass" for the manufacture of fine paper, was collected at the foot of the Asirgarh Fort. The views around the Fort show the typical open, dry deciduous forest with *Boswellia serrata*, quite prominent among the trees and *Cymbopogon*, among the grasses.

In general, the vegetation is a typical dry deciduous type with the "Sal", "Teak", and "Anjan" as the main components. But, some of the patches in Pachmarhi and the neighbouring peaks with high moisture and good shade, which are ideally suited for the development of some of the subtropical and even temperate plants, may be considered only as a local phase from the general vegetational type. Interestingly enough, members of Rosaceæ and epiphytic orchids appear to be very rare in this area. Climbers are comparatively few. Apart from the plants mentioned by Witt (1916), many species of Malvaceæ, Papilionaceæ, Compositæ, Boraginaceæ, Solanaceæ, Acanthaceæ, Labiateæ, Amaranthaceæ, Euphorbiaceæ, Orchidaceæ, and Gramineæ have been collected from these areas. A good collection of plants of many families which are not mentioned by Witt (*l.c.*) such as Umbelliferæ, Scrophulariaceæ, Commelinaceæ, Araceæ and Cyperaceæ has been made. Quite a good number of ferns has been recorded from the Pachmarhi Zone.

The occurrence of Himalayan plants like *Thalictrum*, *Chirita*, *Ceropegia*, *Remusatia* and several others as shown in the enumerated list below on the Pachmarhi plateau and the surrounding peaks, though quite interesting, does not signify anything sensational. Similar occurrence of the Himalayan species on the various hill-tops of Chota Nagpur and surroundings and on Mahendragiri, Gudem ranges and surroundings of the Eastern Ghats of the Orissa and Andhra States has been reported by several workers. These are instances of either discontinuous distribution, or remnants of vegetation of bygone days, got isolated on account of ancient geological disturbances.

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SYSTEMATIC ENUMERATION OF THE SPECIES COLLECTED AND STUDIED PTERIDOPHYTES

[The following collections made from Pachmarhi and surroundings by Major Dixit are in no way complete. The nomenclature followed is according to R. E. Holttum, '*Flora of Malaya*, Vol. II. Ferns, 1954.]

OPHIOGLOSSACEÆ
Ophioglossum sp.
OSMUNDACEÆ
Osmunda regalis Linn.
GLEICHENIACEÆ
Gleichenia linearis (Burm.) Clarke
PTERIDACEÆ
Adiantum philippense Linn.
(= *A. lunulatum* Burm.)
Pteris quadro-aurita Retz.
P. biaurita Linn.
(= *Campteria biaurita* Hook.)
Aleuritopteris farinosa (Forsk.) Fée
[= *Cheilanthes farinosa* (Forsk.) Kaulf.]
Cheilanthes tenuifolia Sw.
Sphenomeris chusana (L.) Copel.
(= *Stenoloma chinensis* Bedd.)
CYATHEACEÆ
Cyathea gigantea (Wall.) Holtt.
(= *Alsophila glabra* Hook.)
C. latebrosa (Wall.) Copel.
(= *A. latebrosa* Hook.)
ASPIDIACEÆ
Tectaria macrodonta (Fée) C. Chr.
Athyrium macrocarpum Bl. var. *atkinsonia* C.B.Cl.
Abacopteris urophylla (Wall.) Ching
(= *Dryopteris urophylla* C. Chr.)
Cyclosorus sp.
(= *Dryopteris mollis* Hiern.)
BLECHNACEÆ
Blechnum orientale Linn.
POLYPODIACEÆ
Leptochilus decurrens Bl.
(= *Gymnopteris variabilis* Hook.)
Pyrrosia sp.
(= *Pleopeltis linearis* Thunb.)
EQUISETACEÆ
Equisetum debile Roxb.
SELAGINELLACEÆ
Selaginella bryopteris (Linn.) Baker

ANGIOSPERMS

*—Not recorded by D. O. Witt (probably being of no economic value).

( )—Region where collected.

(E,W,S)—Indicating occurrence of the species in the Eastern Himalayas including Assam hills (E), the Western Himalayas (W) and the Southern hills including Parasnath and Orissa hills (S)

RANUNCULACEÆ

Clematis triloba Heyne (Duphgarh) (S)

Naravelia zeylanica DC. (Duphgarh)

* *Thalictrum foliolosum* DC. (Around Pachmarhi) (E, W)

DILLENIACEÆ

Dillenia pentagyna Roxb. (Around Pachmarhi)

MAGNOLIACEÆ

Michelia champaca Linn. (Mahadev Hill)

MENISPERMACEÆ

Cissampelos pareira Linn. (Pachmarhi; Mahadev Hill)

BERBERIDACEÆ

Berberis asiatica Roxb. (Around Pachmarhi) (E, W, S)

CAPPARIDACEÆ

* *Cleome chelidonii* Linn.f. (Khandwa)

* *Cleome viscosa* Linn. (Khandwa)

VIOLACEÆ

* *Hybanthus enneaspermus* (Linn.) F. Muell. (Chindwara)
(= *Ionidium suffruticosum* Ging.)

FLACOURTIACEÆ

Flacourtia indica (Burm.f.) Merr. (Duphgarh)
(= *Flacourtia ramontchi* L'Herit.)
(= F. *ramontchi* L'Herit. var. *sapida* Hook. f. and Thom.)

POLYGALACEÆ

* *Polygala chinensis* Linn. (Khandwa)

* *Polygala elongata* Klein. (Khandwa)

CARYOPHYLLACEÆ

Polycarpæa corymbosa (Linn.) Lamk. (Mahadev Hill)

DIPTEROCARPACEÆ

Shorea rubusta Gaertn. (Mahadev Hill)

MALVACEÆ

* *Hibiscus lobatus* O. Ktz. (Mahadev Hill; Chindwara)
(= *H. solandra* L'Herit.)

Kydia calycina Roxb. (Around Pachmarhi; Chindwara)

Sida acuta Burm. f. (Pachmarhi)
(= *S. carpinifolia* Linn.f.)

Sida cordifolia Linn. (Mahadev Hill)

* *Sida veronicæfolia* Lamk. (Khandwa)
(= *Sida humilis* Willd.)

Sida rhombifolia Linn. (Pachmarhi)

Sida rhombifolia Linn. var. *rhomboidea* Mast. (Around Pachmarhi)
(= *S. rhomboidea* Roxb.)

Sida spinosa Linn. (Khandwa)

BOMBACACEÆ

Salmalia malabarica (DC.) Schott. & Endl. (Duphgarh)
(= *Bombax malabaricum* DC.)

STERCULIACEÆ

Firmiana colorata (Roxb.) R.Br. (Duphgarh)
[= *Erythropsis colorata* (Roxb.) Burkill]
(= *Sterculia colorata* Roxb.)

Helicteres isora Linn. (Duphgarh)

Sterculia urens Roxb. (Khandwa)

Sterculia villosa Roxb. (Around Pachmarhi)

Waltheria indica Linn. (Pachmarhi; Mahadev Hill)

TILIACEÆ

Corchorus olitorius Linn. (Khandwa)

Grewia elastica Royle (Duphgarh)
(= *G. asiatica* Mast. var. *vestita* Wall.)

Grewia flavescens Juss. (Pachmarhi)
[= *Vinticena flavescens* (Juss.) Burret]

Grewia subinæqualis DC. (Pachmarhi)
[= *G. asiatica* auct. (non Linn.)]

Triumfetta bartramia Linn. (Pachmarhi)
(= *T. rhomboidea* Jacq.)

Triumfetta pilosa Roth. (Duphgarh; Around Pachmarhi)

BALSAMINACEÆ

* *Impatiens balsamina* Linn. (Pachmarhi)

* *Impatiens inconspicua* Benth. (Duphgarh) (S)

* *Impatiens kleinii* Wt. & Arn. (Mahadev Hill) (S)

OXALIDACEÆ

* *Oxalis corniculata* Linn. (Pachmarhi; Mahadev Hill)

RUTACEÆ
Murraya paniculata (Linn.) Jack (Pachmarhi)
(= *M. exotica* Linn.)
SIMARUBACEÆ
Ailanthus excelsa Roxb. (Khandwa)
BURSERACEÆ
Boswellia serrata Roxb. (Khandwa)
MELIACEÆ
Chloroxylon swietenia DC. (Pachmarhi)
CELASTRACEÆ
Elaeodendron glaucum Pers. (Pachmarhi)
Celastrus paniculata Willd. (Around Pachmarhi)
RHAMNACEÆ
Helinus lanceolatus Brandis (Duphgarh)
Rhamnus wightii Wt. & Arn. (Duphgarh)
Zizyphus xylopyra (Retz.) Willd. (Pachmarhi)
VITACEÆ
Ampelocissus latifolia (Roxb.) Planch. (Khandwa)
(= *Vitis latifolia* Roxb.)
* *Ampelocissus tomentosa* Planch. (Chindwara)
(= *Vitis tomentosa* Heyne)
Cayratia carnosa Gagnep. (Khandwa)
(= *Vitis carnosa* Wall.)
Cissus repanda Vahl (Around Pachmarhi)
(= *Vitis repanda* Wt. & Arn.)
Cissus vitiginea Linn. (Khandwa)
(= *Vitis linnæi* Wall.)
Leea edgeworthii Santapau (Duphgarh)
(= *Leea aspera* Edgew.)
SAPINDACEÆ
Dodonaea viscosa (Linn.) Jacq. (Pachmarhi; Mahadev Hill)
ANACARDIACEÆ
Buchanania lanzan Spreng. (Pachmarhi; Mahadev Hill)
(= *B. latifolia* Roxb.)
Lannea coromandelica (Houtt.) Merr. (Chindwara)
[= *Lannea grandis* (Dennst.) Engl.]
(= *Odina woodier* Roxb.)
Rhus parviflora Roxb. (Pachmarhi)
PAPILIONACEÆ
Abrus precatorius Linn. (Khandwa)
* *Alysicarpus bupleurifolius* (Linn.) DC. (Khandwa)
* *Alysicarpus bupleurifolius* (Linn.) DC. var. *gracilis* Baker (Chindwara) (S)
* *Alysicarpus vaginalis* (Linn.) DC. (Mahadev Hill)
Butea superba Roxb. (Chindwara)
* *Calpurnea aurea* Baker (Around Pachmarhi) (S)
Clitoria ternatea Linn. (Khandwa)
* *Crotalaria albida* Heyne *ex* Roth (Mahadev Hill; around Pachmarhi)
(= *C. epunctata* Dalz.)
* *Crotalaria linifolia* Linn.f. (Chindwara)
Desmodium motorium (Houtt.) Merr. (Mahadev Hill)
[= *Desmodium gyrans* (Linn.f) DC.]
Desmodium laxiflorum DC. (Mahadev Hill)
* *Desmodium triflorum* (Linn.) DC. (Chindwara)
Erythrina suberosa Roxb. (Pachmarhi)
* *Erythrina stricta* Roxb. (Around Pachmarhi)
* *Galactia villosa* Wt. & Arn. (Pachmarhi) (S)
* *Heylandia latebrosa* (Linn.) DC. (Khandwa)
* *Indigofera enneaphylla* Linn. (Around Pachmarhi)
Indigofera glandulosa Willd. (Khandwa)
Indigofera hirsuta Linn. (Chindwara)
* *Indigofera linifolia* Retz. (Around Pachmarhi)
Indigofera pulchella Roxb. (Pachmarhi)
Indigofera subulata Vahl (Chindwara)
Indigofera trifoliata Linn. (Chindwara)
Indigofera trita Linn.f. (Chindwara)
Millettia auriculata Baker (Around Pachmarhi; Chindwara)
Moghania bracteata (Roxb.) H. L. Li (Pachmarhi)
(= *Flemingia bracteata* Wt.)
Moghania macrophylla (Willd.) O. Ktz. (Mahadev Hill)
(= *Flemingia congesta* Roxb.)
Moghania strobilifera (Linn.) St. Hill ex Jacks (Pachmarhi)
(= *Flemingia strobilifera* R. Br. *ex* Ait.)
Ougeinia oojeinensis (Roxb.) Hochreut (Mahadev hill; Chindwara)
(= *Ougeinia dalbergioides* Benth.)
* *Phaseolus calcaratus* Roxb. (Pachmarhi)
Phaseolus trilobus Ait. (Khandwa)
* *Psoralea corylifolia* Linn. (Khandwa)

Pterocarpus marsupium Roxb. (Around Pachmarhi; Chindwara)
* *Rhynchosia minima* (Linn.) DC. (Khandwa)
* *Sophora interrupta* Bedd. (Pachmarhi) (S)
* *Tephrosia hookeriana* Wt. & Arn. (not of F. B. I.) (Khandwa)
Tephrosia purpurea Pers. (Pachmarhi)
* *Tephrosia tenuis* Wall. (Chindwara)
Teramnus labialis Spreng. (Around Pachmarhi)
Vigna capensis Walp. (Duphgarh; Mahadev Hill)
(= *Vigna vexillata* A. Rich.)
* *Zornia diphylla* Pers. (Mahadev Hill)

CÆSALPINIACEÆ
Bauhinia racemosa Lamk. (Chindwara; Khandwa)
Cassia mimosoides Linn. (Duphgarh; around Pachmarhi)
Hardwickia binata Roxb. (Khandwa).

MIMOSACEÆ
Acacia chundra (Roxb.) Willd. (Khandwa)
(= *Acacia sundra* DC.)
Acacial eucophlæa Willd. (Khandwa)
* *Acacia torta* (Roxb.) Craib (Pachmarhi; Khandwa)
[= *Acacia cæsia* Wt. & Arn. (*non* Willd.)]
Albizzia odoratissima (Linn.f.) Benth. (Pachmarhi; Duphgarh; Mahadev Hill)
Mimosa hamata Willd. (Khandwa)
Mimosa rubicaulis Lamk. (Khandwa)

COMBRETACEÆ
Anogeissus latifolia (Roxb.) Wall. (Chindwara)
Anogeissus pendula Edg. (Pachmarhi)
Terminalia bellerica (Gaertn.) Roxb. (Chindwara)
Terminalia chebula Retz. (Pachmarhi)
Terminalia tomentosa Wt. & Arn. (Pachmarhi)
(= An *Terminalia crenulata* Roth?)

MYRTACEÆ
Syzygium cumini (Linn.) Skeels (Betul)
(= *Eugenia jambolana* Lamk.)

LECYTHIDACEÆ
Careya arborea Roxb. (Chindwara)

MELASTOMACEÆ
Melastoma malabathricum Linn. (Around Pachmarhi)

LYTHRACEÆ
Lagerstræmia parviflora Roxb. (Chindwara)
Lawsonia inermis Linn. (Chindwara)
(= *Lawsonia alba* Lamk.)

ONAGRACEÆ
Jussiaea suffruticosa Linn. (Around Pachmarhi)

SAMYDACEÆ
Casearia graveolens Dalz. (Pachmarhi)
Casearia tomentosa Roxb. (Chindwara)

CUCURBITACEÆ
* *Bryonopsis laciniosa* (Linn.) Naud. (Chindwara)
(= *Bryonia laciniosa* Linn.)
Melothria heterophylla (Lour.) Cogn. (Duphgarh; Mahadev Hill; Around Pachmarhi)
(= *Zehneria umbellata* Thw.)
* *Melothria leiosperma* (Wt. & Arn.) Cogn. (Duphgarh) (S)
(= *Mukia leiosperma* Wt. & Arn.)
Melothria maderaspatana (Linn.) Cogn. (Khandwa)
(= *Mukia scabrella* Arn.)
Trichosanthes cucumerina Linn. (Chindwara)

BEGONIACEÆ
* *Begonia picta* Sm. (Pachmarhi; Duphgarh) (S)

MOLLUGINACEÆ
* *Glinus oppositifolia* (Linn.) A. DC. (Around Pachmarhi)
(= *Mollugo oppositifolia* Linn.)
(= *Mollugo spergula* Linn.)
* *Mollugo pentaphylla* Linn. (Duphgarh)
(= *Mollugo stricta* Linn.)

UMBELLIFERÆ
* *Bupleurum mucronatum* Wt. & Arn. (Pachmarhi; Duphgarh)
* *Centella asiatica* (Linn.) Urban. (Mahadev Hill)
(= *Hydrocotyle asiatica* Linn.)
* *Pimipnella heyneana* Wall. (Pachmarhi; Duphgarh)

ARALIACEÆ
Schefflera venulosa (W. & A.) Harms. (Duphgarh)
(= *Heptapleurum venulosum* Seem; F.B.I. in part)

CORNACEÆ
Alangium salvifolium (Linn.f.) Wang. (Chindwara)
(= *Alangium lamarckii* Thw.)

RUBIACEÆ
Adina cordifolia (Roxb.) Hook.f. (Duphgarh)
* *Argostemma sarmentosum* Wall. (Pachmarhi) (W, E)
* *Borreria hispida* (Linn.) Schum. (Mahadev Hill)
(= *Spermacoce hispida* Linn.)

* *Borreria stricta* (Linn.f.) Schum. (Mahadev Hill)
(= *Spermacoce stricta* Linn.f.)
Gardenia latifolia Ait. (Duphgarh; Around Pachmarhi; Chindwara)
Gardenia turgida Roxb. (Chindwara)
Mitragyna parvifolia (Roxb.) Korth. (Chindwara)
(= *Stephegyne parvifolia* Korth.)
* *Oldenlandia corymbosa* Linn. (Chindwara)
Randia longispina Wt. & Arn. (Chindwara)
(= *Randia dumetorum* Lamk.; F.B.I. in part)

COMPOSITÆ
* *Acanthospermum hispidum* DC. (Mahadev Hill)
* *Ageratum conyzoides* Linn. (Duphgarh)
* *Artemisia parviflora* Buch-Ham. *ex* Roxb. (Mahadev Hill)
* *Bidens biternata* (Lour.) Merr. & Sherff. (Mahadev Hill)
(= *Bidens pilosa* auct. *non* Linn. var. *bipinnata* Hook.f.)
* *Eclipta prostrata* (Linn.) Linn. (Mahadev Hill; Khandwa)
[= *Eclipta alba* (Linn.) Hassk.]
* *Emilia sonchifolia* (Linn.) DC. (Mahadev Hill; Khandwa)
* *Glossocardia bosvallea* (Linn.f.) DC. (Khandwa)
(= *Glossocardia linearifolia* Cass.)
* *Lagascea mollis* Cav. (Chindwara; Khandwa)
* *Pulicaria wightiana* (DC.) Benth. *ex* Clarke (Mahadev Hill)
* *Vernonia cinerea* (Linn.) Less. (Pachmarhi)
Vernonia divergens (Roxb.) Edg. (Duphgarh)
* *Vicoa indica* (Willd.) DC. (Pachmarhi; Khandwa)
(= *Vicoa auriculata* Cass.)

CAMPANULACEÆ
* *Lobelia leschenaultiana* (Presl.) Skottsb. (Duphgarh) (S)
(= *Lobelia excelsa* Lesch.)
* *Lobelia nicotianæfolia* Heyne (Pachmarhi) (S)

MYRSINACEÆ
Embelia tsjeriam—cottam (R. & S.) A. DC. (Pachmarhi)
(= *Embelia robusta* Clarke in F.B.I., *non* Roxb.)

SAPOTACEÆ
Manilkara hexandra (Roxb.) Dub. (Pachmarhi) (with naturally variegated leaves—green and yellow)
(= *Mimusops hexandra* Roxb.)

EBENACEAE
Diospyros melanoxylon Roxb. (Chindwara)

OLEACEÆ
Jasminum arborescens (Roxb.) (Duphgarh) (S)
Jasminum grandiflorum Linn. (Pachmarhi) (S)
* *Jasminum roxburghianum* Wall. (Pachmarhi) (S)
Jasminum sambac Ait. (Pachmarhi)
Nyctanthes arbor-tristis Linn. (Chindwara)

APOCYNACEÆ
Carissa spinarum A. DC. (Chindwara)
Ichnocarpus frutescens R. Br. (Pachmarhi)
Wrightia tinctoria R. Br. (Pachmarhi)

ASCLEPIADACEÆ
* *Ceropegia hirsuta* Wt. & Arn. (Chindwara) (S)
(= *Ceropegia vincæfolia* Hooker)
* *Ceropegia macrantha* Wt. (Duphgarh) (W, E)
Cryptostegia grandiflora (Roxb.) R. Br. (Khandwa)
* *Gymnema hirsutum* Wt. & Arn. (Around Pachmarhi) (S)
Gymnema sylvestre (Willd.) R. Br. (Duphgarh)
Hemidesmus indicus (Willd.) R. Br.
Leptadenia reticulata Wt. & Arn. (Chindwara)
Marsdenia tenacissima Wt. & Arn. (Chindwara)

GENTIANACEÆ
* *Canscora diffusa* R. Br. (Mahadev Hill)
* *Exacum pedunculatum* Linn. (Chindwara)
* *Limnanthemum cristatum* (Roxb.) Griseb. (Khandwa)
* *Swertia minor* Knobl. (Duphgarh)

BORAGINACEÆ
* *Cynoglossum furcatum* Wall. (Mahadev Hill)
* *Cynoglossum micranthum* Desf. (Duphgarh) (E, W)
* *Cynoglossum* sp. (Duphgarh)
* *Heliotropium brevifolium* Wall. (Pachmarhi)
(= *Heliotropium strigosum* Willd. var. *brevifolia* Cl.)
* *Heliotropium indicum* Linn. (Chindwara)
* *Trichodesma amplexicaule* Roth (Khandwa)
* *Trichodesma indicum* R. Br. (Duphgarh; Mahadev Hill)

CONVOLVULACEÆ

Argyreia nervosa (Burm.f.) Boj. (Around Pachmarhi)
(= *Argyreia speciosa* Sweet)

Cuscuta reflexa Roxb. (Around Pachmarhi)

* *Evolvulus alsinoides* Linn. (Pachmarhi; Duphgarh; Mahadev Hill)

* *Ipomæa aquatica* Forsk. (Khandwa)

Merremia emarginata (Burm.f.) Hall. (Khandwa)

SOLANACEÆ

Datura metel Linn. (Khandwa)
(= *Datura fastuosa* Linn.)

* *Physalis minima* Linn. var. *indica* Cl. (Chindwara; Khandwa)

* *Solanum dulcamara* Linn. (Mahadev Hill) (E, W)

Solanum indicum Linn. (Pachmarhi; Mahadev Hill)

* *Solanum melongena* Linn. var. *insanum* Prain (Chindwara)

* *Solanum nigrum* Linn. (Duphgarh)

* *Solanum xanthocarpum* Schrad. & Wendl. (Chindwara)

SCROPHULARIACEÆ

* *Alectra thomsonii* Hook.f. (Around Pachmarhi) (S)

* *Bacopia monnieri* (Linn.) Pennell (Khandwa)
(= *Herpestis monniera* Benth.)

* *Dopatrium junceum* Ham. (Chindwara)

* *Kickxia incana* (Wall.) Pennell (Around Pachmarhi) (W)
(= *Linaria incana* Wall.)

* *Kickxia ramosissima* (Wall.) Janchen (Around Pachmarhi)
(= *Linaria ramosissima* Wall.)

* *Limnophila rugosa* (Roth) Merr. (Around Pachmarhi)
(= *Limnophila roxburghii* G. Don)

* *Limnophila* sp. (Mahadev Hill)

* *Lindernia crustacea* (Linn.) F. V. Mueller (Duphgarh)
[= *Vandellia crustacea* (Linn.) Benth.]

* *Mimulus strictus* Benth. (Chindwara) (W)
(= *Mimulus gracilis* auct. plur. *non* R. Br.)

* *Scoparia dulcis* Linn. (Pachmarhi)

* *Striga euphrasioides* (Vahl) Benth. (Chindwara)

LENTIBULARIACEÆ

* *Utricularia wallichiana* Wt. (Pachmarhi)

GESNERIACEÆ

* *Chirita bifolia* Don (Pachmarhi) (W, E)

MARTINIACEÆ

* *Martinia annua* Linn. (Chindwara)
(= *Martinia diandra* Glox.)

PEDALIACEÆ

* *Sesamum indicum* Linn. (Chindwara; Khandwa)

ACANTHACEÆ

* *Andrographis echioides* Nees (Chindwara)

Asteracantha longifolia (Linn.) Nees (Khandwa)
(= *Hygrophila spinosa* Anders.)

Barleria cristata Linn. (Mahadev Hill)

Carvia callosa (Nees) Bremek. (Duphgarh)
(= *Strobilanthes callosus* Nees)

Dipteracanthus beddomei (Clarke) Santapau (Chindwara)
(= *Ruellia beddomei* Cl.)

* *Dipteracanthus suffruticosus* (Roxb.) Voigt. (Chindwara)
(= *Ruellia suffruticosa* Roxb.)

* *Ecbolium linneanum* Kurz (Chindwara)

* *Hemigraphis latebrosa* Nees (Pachmarhi)

Justicia betonica Linn. (Pachmarhi)

* *Justicia diffusa* Willd. (Duphgarh)

* *Justicia prostrata* Gamble (Around Pachmarhi)

* *Rostellularia procumbens* (Linn.) Nees (Pachmarhi)
(= *Justicia procumbens* Linn.)

* *Strobilanthes walkeri* Nees (Around Pachmarhi) (S)

* *Thunbergia alata* Boj. (Pachmarhi)

VERBENACEÆ

Clerodendrum phlomidis Linn.f. (Khandwa)

Clerodendrum serratum (Linn.) Moon (Chindwara)

Gmelina arborea Roxb. (Around Pachmarhi; Khandwa)

Lantana camara Linn. var. *aculeata* (Linn.) Moldenke (Chindwara)
(= *Lantana aculeata* Linn.
= *Lantana camara* auct. *non* Linn.)

* *Phyla nodiflora* (Linn.) Green. (Khandwa)
(= *Lippia nodiflora* Rich.)

Premna barbata Wall. (Pachmarhi)

Tectona grandis Linn.f. (Chindwara)

Vitex negundo Linn. (Chindwara)

LABIATÆ

* *Anisomeles indica* (Linn.) O. Ktz. (Mahadev Hill)
(= *Anisomeles ovata* R.Br.)

* *Hyptis suaveolens* Poit. (Chindwara)

Lavandula bipinnata (Roth) O. Ktz. var. *rothiana* O. Ktz. (Khandwa)
(= *Lavandula burmanni* Benth.)

* *Leucas aspera* Spreng. (Chindwara)
* *Leucas cephalotes* Spreng. (Chindwara)
* *Leucas lanata* Benth. (Around Pachmarhi) (W, S)
* *Leucas mollissima* Wall. var. *scaberula* Hook.f. (Around Pachmarhi)
* *Micromeria biflora* Benth. (Duphgarh; Mahadev Hill) (E, W, S)
Ocimum basilicum Linn. (Khandwa)
* *Orthosiphon rubicundus* Benth. (Chindwara)
* *Plectranthus mollis* (Ait.) Spreng. (Mahadev Hill; Around Pachmarhi)
(= *Plectranthus incanus* Link.)
Pogostemon plectranthoides Desf. (Pachmarhi)

NYCTAGINACEÆ
* *Bœrhaavia diffusa* Linn. (Chindwara; Khandwa)
(= *Bœrhaavia repens* Linn.)
* *Mirabilis jalapa* Linn. (Khandwa)

AMRANTHACEÆ
* *Achyranthes aspera* Linn. var. *rubro-fusca* Hook.f. (Pachmarhi) (S)
* *Achyranthes bidentata* R.Br. (Around Pachmarhi) (E,W, S)
* *Aerva lanata* (Linn.) Juss (Khandwa)
* *Aerva monsoniæ* (Linn.f.) Mart. (Khandwa)
* *Alternanthera sessilis* (Linn.) R. Br. (Mahadev Hill; Khandwa)
Celosia cristata Linn. (Mahadev Hill)
* *Gomphrena celosioides* Mart. (Mahadev Hill)
* *Pupalia lappacea* (Linn.) Juss. (Around Pachmarhi; Khandwa)

CHENOPODIACEÆ
Basella rubra Linn. (Khandwa)

POLYGONACEÆ
Polygonum glabrum Willd. (Chindwara)

LAURACEÆ
* *Cassytha filiformis* Linn. (Chindwara)
Litsea glutinosa (Lour.) C. B. Robinson (Duphgarh; Around Pachmarhi)
(= *Litsea chinensis* Lamk. = *Litsea sebifera* Pers.)

LORANTHACEÆ
Dendrophthœ falcata (Linn.f.) Etting. (Around Pachmarhi)
(= *Loranthus longiflorus* Desr.)
Scurrula parasitica Linn. (Pachmarhi)
(= *Loranthus scurrula* Linn.)
Viscum articulatum Burm.f. (Around Pachmarhi)
(= *V. nepalense* Spreng.)

SANTALACEÆ
Osyris wightiana Wall. *ex* Wight (Duphgarh)
(= *Osyris arborea* Wall. *ex* A.DC.)

EUPHORBIACEÆ
* *Acalypha ciliata* Forsk. (Chindwara, Khandwa)
* *Acalypha malabarica* Muell.—Arg. (Chindwara)
Antidesma diandrum Roth. (Mahadev Hill)
Briedelia retusa Spreng. (Khandwa)
Emblica officinalis Gaertn. (Mahadev Hill)
(= *Phyllanthus emblica* Linn.)
* *Euphorbia dracunculoides* Linn. (Mahadev Hill)
* *Euphorbia geniculata* Orteg. (Chindwara; Khandwa)
* *Euphorbia hirta* Linn. (Chindwara)
* *Euphorbia hypericifolia* Linn. (Duphgarh; Khandwa)
Euphorbia neriifolia Linn. (Duphgarh; Around Pachmarhi)
Euphorbia nivulia Buch.-Ham. (Around Pachmarhi)
Glochidion velutinum Wt. (Pachmarhi; Mahadev Hill)
Homonoia riparia Lour. (Chindwara)
Jatropha curcas Linn. (Chindwara)
Mallotus philippensis Muell.-Arg. (Pachmarhi)
(= *Mallotus philippinensis* auct. plur. per Sphalm.)
* *Phyllanthus debilis* Ham. (Duphgarh) (E, W, S)
* *Phyllanthus simplex* Retz. (Chindwara)
* *Phyllanthus urinaria* Linn. (Khandwa)
* *Sauropus quadrangularis* Muell.-Arg. (Khandwa)
Securinega virosa (Roxb. *ex* Willd.) Pax. & Hoffm. (Duphgarh)
(= *Flueggea microcarpa* Bl.)

ULMACEÆ
Trema orientalis (Linn.) Bl. (Pachmarhi)
Trema politoria Planch. (Chindwara)

URTICACEÆ
Bœhmeria scabrella (Roxb.) Gaud. (Mahadev Hill)
(= *Bœhmeria platyphylla* Don)
* *Fleurya interrupta* (Linn.) Gaud. (Duphgarh; Mahadev Hill)
* *Lecanthus peduncularis* (Wall.) Wedd. (Duphgarh)

MORACEÆ
Ficus arnottiana Miq. (Chindwara)
Ficus gibbosa Bl. (Chindwara)
Ficus glomerata Roxb. (Chindwara)

Ficus tomentosa Linn. (Chindwara)

HYDROCHARITACEÆ

* *Ottelia alismoides* (Linn.) Pers. (Khandwa)

* *Vallisneria spiralis* Linn. (Khandwa)

ORCHIDACEÆ

* *Geodorum densiflorum* Schlec. (Duphgarh)
(= *Geodorum dilatatum* R. Br.)

* *Goodyera procera* Hook. (Pachmarhi) (E, W, S)

* *Habenaria constricta* Hook.f. (Pachmarhi) (E)

* *Habenaria digitata* Lindl. (Pachmarhi; Duphgarh)

* *Habenaria grandiflora* Lindl. (Pachmarhi)

* *Habenaria plantaginea* Lindl. (Chindwara)

* *Habenaria platyphylla* Spreng. (Chindwara)

* *Microstylis versicolor* Lindl. (Around Pachmarhi)
(= *Microstylis rheedii* Wt.)

* *Peristylus stocksii* (Hook.f.) Kraenz (Duphgarh)

* *Vanda parviflora* Lindl. (Pachmarhi)

ZINGEBERACEÆ

* *Costus speciosus* Smith (Chindwara)

* *Curcuma decipiens* Dalz. (Duphgarh; Around Pachmarhi) (S)

HYPOXYDACEÆ

Curculigo orchioides Gaertn. (Chindwara)

* *Hypoxis aurea* Lour. (Duphgarh).

DIOSCOREACEÆ

Dioscorea oppositifolia Linn. (Duphgarh; Around Pachmarhi)

* *Dioscorea pentaphylla* Linn. var. *linnæi* Prain (Mahadev Hill)

* *Dioscorea sativa* Linn. (Chindwara)

LILIACEÆ

Asparagus racemosus Willd. (Duphgarh; Khandwa)

Gloriosa superba Linn. (Mahadev Hill)

* *Iphigenia indica* (Linn.) A. Gray (Duphgarh)

SMILACEÆ

* *Smilax zeylanica* Linn. (Chindwara)

COMMELINACEÆ

* *Commelina forskalii* Vahl (Khandwa)

* *Commelina diffusa* Burm.f. (Chindwara)
(= *Commelina nudiflora* auct. *non* Linn.)

* *Commelina paludosa* Bl. (Duphgarh; Mahadev Hill; Khandwa)
(= *Commelina obliqua* Buch.-Ham. *ex.* Don)

* *Cyanotis cristata* (Linn.) D. Don (Mahadev Hill; Chindwara)

* *Cyanotis fasciculata* (Heyne *ex.* Roth.) Schult.f. (Khandwa)

PALMÆ

Phœnix humilis Royle (Pachmarhi)

TYPHACEÆ

* *Typha angustata* Bory & Chaub. (Khandwa)

ARACEÆ

* *Plesmonium margaritiferum* Schott. (Duphgarh) (S)

* *Remusatia vivipara* (Roxb.) Schott. (Duphgarh) (E,W, S)

LEMNACEÆ

* *Lemna polyrrhiza* Linn. (Khandwa)

ERIOCAULACEÆ

* *Eriocaulon longicuspis* Hook.f. var. *polycephala* Fyson (Pachmarhi) (S)

* *Eriocaulon oryzetorum* Mart. (Around Pachmarhi) (E, W)

* *Eriocaulon sieboldianum* Sieb. & Zucc. (Chindwara)

CYPERACEÆ

* *Bulbostylis barbata* Kunth. (Chindwara)

* *Carex filicina* Nees (Duphgarh)

* *Cyperus compressus* Linn. (Chindwara)

* *Cyperus exaltatus* Retz. (Khandwa)

* *Cyperus imbricatus* Retz. (Pachmarhi)
(= *Cyperus radiatus* Vahl)

* *Cyperus iria* Linn. (Chindwara; Khandwa)

* *Cyperus kyllinga Endl.* (Pachmarhi)
(= *Kyllinga monocephala* Rottb.)

* *Cyperus michelianus* (Linn.) Link. sub-sp. *pygmæus* (Rottb.) Aschers. & Graebn. (Khandwa)
(= *Cyperus pygmæus* Rottb.)

* *Cyperus rotundus* Linn. (Khandwa)

* *Cyperus uncinatus* Poir (Mahadev Hill; Around Pachmarhi)
(= *Cyperus cuspidatus* H. B. K.)

* *Eriophorum comosum* Wall. (Khandwa, Asirgarh Fort)

* *Fimbristylis diphylla* Vahl (Mahadev Hill)

* *Fimbristylis ferruginea* Vahl (Khandwa)

* *Fimbristylis miliacea* Vahl (Khandwa)

* *Fimbristylis monostachya* Hassk. (Khandwa)

* *Liphocarpa argentea* R.Br. (Around Pachmarhi) (E, W- S)

* *Mariscus cyperinus* Vahl (Pachmarhi)

* *Scirpus squarrosus* Linn. (Around Pachmarhi)

* *Scleria lithosperma* Sw. (Around Pachmarhi)

GRAMINEÆ

* *Alloteropsis cimicina* Stapf (Chindwara)

Apluda aristata Linn. (Duphgarh; Khandwa)

Aristida setacea Retz. (Chindwara; Khandwa)

Bambusa arundinacea Willd. (Chindwara)

* *Brachiaria eruciformis* Griseb. (Khandwa)

* *Brachiaria ramosa* Stapf (Mahadev Hill; Khandwa)

Chloris virgata Sw. (Khandwa)

Chrysopogon montanus Trin (Khandwa)
(= *Andropogon monticola* Schult. var. *trinii* Hook.f.)

Cymbopogon martini (Roxb.) Wats. (Khandwa, Asirgarh Fort)
(= *Andropogon schœnanthus* Linn. var. *martini* Hook.f.)

Dactyloctenium ægyptium (Linn.) Beauv. (Khandwa)
(= *Eleusine ægyptiaca* Desf.)

Dendrocalamus strictus Nees (Mahadev Hill; Chindwara)

* *Dicanthium caricosum* A. Camus (Khandwa)

* *Digitaria pedicellaris* Prain (Chindwara)

* *Digitaria pruriens* Buese (Mahadev Hill; Chindwara; Khandwa)

Digitaria stricta Roth *ex.* R. & S. (Pachmarhi)
(= *Digitaria royleana* Prain)
(= *Paspalum royleanum* Nees *ex* Thw.)

Echinochloa colonum (Linn.) Link (Khandwa)
(= *Panicum colonum* Linn.)

Eragrostiella bifaria (Vahl) Bor (Pachmarhi; Around Pachmarhi; Khandwa)
(= *Eragrostis bifaria* Wt. *ex* Steud.)
(= *Erogrostis coromandeliana* Trin)

* *Eragrostis brachyphylla* Stapf (Chindwara)

Eragrostis pilosa (Linn.) Beauv. (Chindwara)

Eragrostis tenuifolia Hochst. (Around Pachmarhi)

* *Eragrostis unioloides* (Retz.) Nees (Mahadev Hill; Chindwara)

* *Eriochloa procera* Hubbard (Chindwara)

* *Hackelochloa granularis* (Linn.f.) O. Ktz. (Chindwara; Khandwa)

Ischæmum pilosum Hack. (Khandwa)

Melanocenchrus jacquemontii Jaub. & Spach. (Khandwa)
(= *Gracillea royleana* Hook.f.)

* *Oplismenus compositus* Beauv. (Duphgarh)

Oryza sativa Linn. (Chindwara)

Panicum miliare Lamk. (Mahadev Hill)

* *Panicum trypheron* Schult. (Around Pachmarhi)

Paspalidium flavidum (Retz.) A. Camus (Chindwara)

Paspalum scrobiculatum Linn. (Mahadev Hill; Around Pachmarhi)

Pennisetum pedicellatum Trin (Pachmarhi)

* *Rhynchelytrum villosum* Chiov. (Around Pachmarhi)

Setaria glauca Beauv. (Khandwa)

Setaria intermedia Roem. & Schult. (Chindwara; Khandwa)

* *Setaria verticillata* Beauv. (Khandwa)

Sorghum vulgare Pers. (Khandwa)

Thysanolæna maxima O. Ktz. (Pachmarhi)
(= *T. agrostis* Nees)

* *Urochloa panicoides* Beauv. (Khandwa)

UNCINULA TECTONAE SALMON ON *TECTONA GRANDIS* L.

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Among the Ascomycetes, members of Erysiphaceae have been given much attention cytologically. A review of all previous work, however, does not show any substantial work on the genus *Uncinula.* Of the four species of *Uncinula* recorded from India by Butler and Bisby in their *Fungi of India* (1931), only two occur in Central India and the Deccan, of these, *U. necator* (Schw.) Burr. shows only the conidial stage, while *U. tectonae* Salmon bears both the conidial and ascigerous stages. *U. necator* caused great loss to the grape growing industry and hence received much attention of the horticulturists, to bring it under control and to eliminate it altogether; while *U. tectonae* does not seem to have received detailed consideration so far, not being acutely destructive.

Ascigerous stages of *Uncinula* are uncommon, probably due to their specificity of suitable climatic, nutritional and genetical conditions. Mundkur (1949) reports in relation to *U. necator*—"the perfect stage is not formed under conditions obtaining in the plains of India, but abundant formation of cleistothecia has been noted in Baluchistan". *U. tectonae* occurs plentifully in Southern India (Butler and Bisby, 1931; Bagchee, 1952). Such infection as was found near Buldana (a hill-station), with lat. 21° and longi. 76°, at an altitude of 2,190 feet from sea-level showed perfect stage in abundance, during winter and it was therefore thought worthwhile studying the morphology, development and cytology of *U. tectonae.*

Material and Methods

Cleistothecia of various developmental stages were available on leaves and could be conveniently made out by the variations in their colour. From young to old, they ranged between white, yellow, orange, brown and black. Material was collected a number of times in 1953, 1954 and 1955. Often two hourly fixings over a period of twenty-four hours during late November–December were made to ensure the possibility of securing successive developmental stages of the fungus. The nuclear divisions in the ascus were mostly obtained from such material as was fixed during late afternoon.

The fixatives used were strong and weak chrome acetic acid, Formalin acetic alcohol, Formalin-propiono-alcohol, Fleming's strong

fluid diluted to half its strength with water and Nawashin's chromic-acetic formalin mixtures (Sass, 1940) as Craf I for the younger and Craf III for the older material. Formalin acetic alcohol, chrome acetic acid (strong) and Craf III gave best results.

The fixed material was washed and processed in the usual manner, to be embedded in paraffin. To secure proper infiltration of paraffin in the silicious, stiff and coriaceous *Tectona* leaf, the period of keeping the material on the bath was a little prolonged. This gave good sections of both the host and parasite in the natural position. Sections were cut 5 μ for the younger and 8–10 μ for the older material as this was found suitable to study developmental sequence of the fungus.

Sections were stained either with Heidenhain's iron-haematoxylin, crystal violet with orange G as counter stain. The former proved more favourable.

Temporary whole mounts were often made of the fungus scrapings or of the crushed cleistothecia in lactophenol, using either acetocarmine or propiono-carmine for staining.

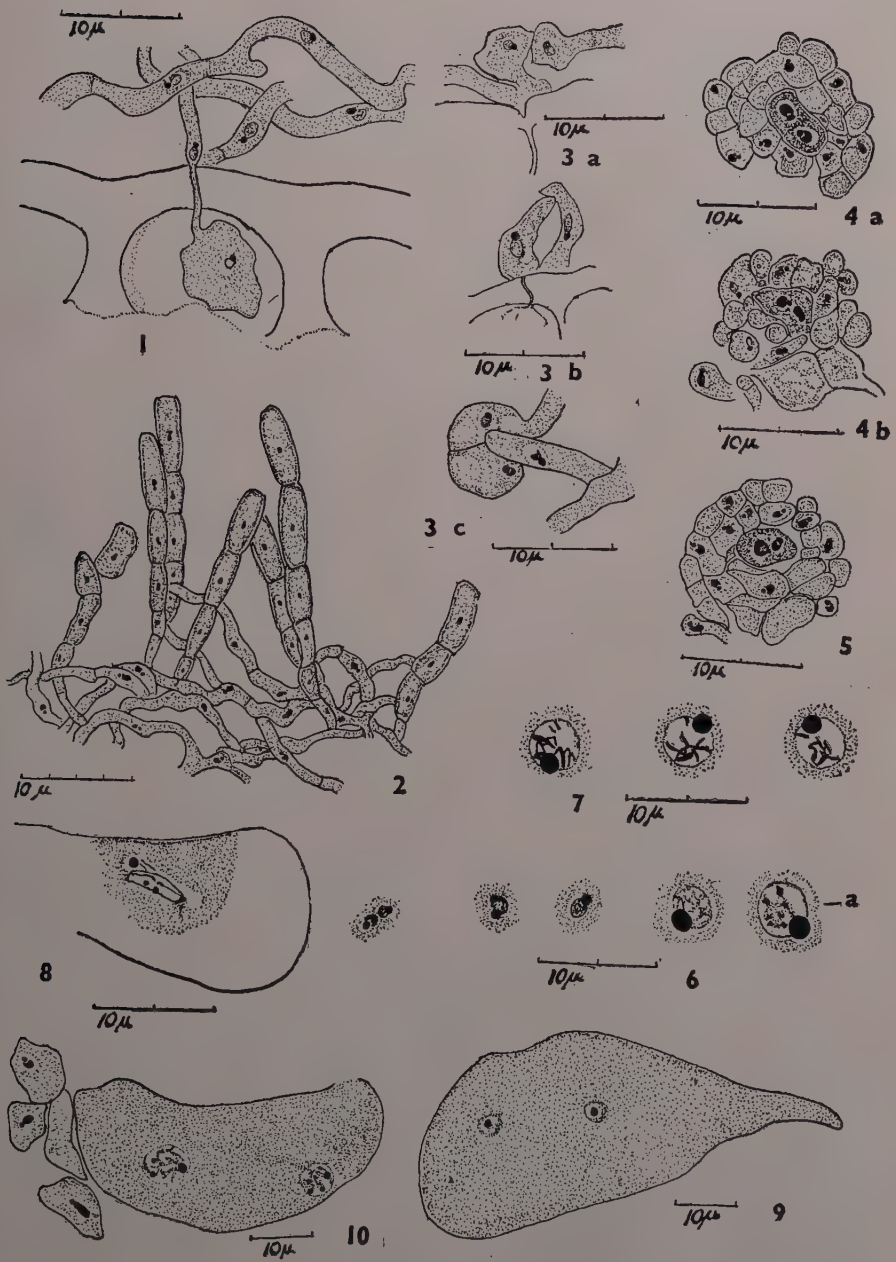
In the later period in this work the author came across the "propiono-carmine staining technique" used by Olive (1950) on *Patella melaloma* and by McGahen and Wheeler (1951) on *Glomerella*. This staining technique was tried in the present work but with no appreciable results.

Observations

The mycelium of *U. tectonae* is restricted to the upper leaf surface of *T. grandis*. It is an ectoparasite, adhering to the host by serrated appresoria. The haustoria are bulbous, uninucleate and, unlike *U. salicis* (D.C.) Wint. are found in the upper epidermal cells only (Text-Fig. 1).

The vegetative hyphae are filamentous, branching, hyaline, septate and usually consist of elongated, tubular, uninucleate or binucleate cells. The hypha is 3 μ wide except in such hyphae from which the conidiophores arise where they are a little broader. The nuclei in the hyphal cells vary in shape and their position in the cells is not constant. The shape of the nucleole remained always round while the 'change' in shape was afforded by nuclear membrane and the chromatin material within.

With the progressive development of the fungus from the middle of October to about the middle of November, the conidiophores bear a chain of conidia formed basipetally (Text-Fig. 2). The conidiophores are unbranched, measure 7·5–9 μ and gradually taper at the base measuring 4·5–6 μ. Conidia are wind-dispersed and germinate by the formation of one or more germ tubes to effect infection. They have been found germinating easily within a day in laboratory preparations of distilled water hanging drops.



TEXT-FIGS. 1–10. Fig. 1. Mycelium and haustorium. Fig. 2. Conidiophores with conidia. Fig. 3. *a*, *b*, *c*. Two hyphal tips in contact with no distinction of an antheridium and an ascogonium. Fig. 4. *a*, *b*. Binucleate central cell with encirc-

ling sheath cells. Fig. 5. Size difference in the nuclei of the binucleate initial cell. Fig. 6. Comparative sizes of two nuclei in the ascus before fusion and of the definitive nucleus, prior to its first division. Fig. 7. Definitive nucleus in the synaptic phase. Fig. 8. First division of the fusion nucleus in metaphase with four bivalents at the equator. Fig. 9. Daughter nuclei of the first division of the definitive nucleus—they are well organised. Fig. 10. The two nuclei increased in size before the second nuclear division in the ascus.

In early November the conidial production declines and there begin to appear tiny white knobs in the fungal felt which is the initiation of the perfect stage. A very large number of slides were cut and whole mounts of the mycelium were also made by lightly removing it from the leaf surface (the latter stained with aceto-carmine or propiono-carmine). These preparations were carefully studied for the stages in the cleistothecial initiation and development. Text-Figures 3 *a*, *b*, *c* represent the often noted contiguous hyphal tips showing no distinction in sexual organization of an antheridium and an ascogonium.

No nuclear migration has been observed between such bodies nor between the vegetative hyphae. It is, therefore, conclusive that *U. tectonae* does not possess any morphologically distinct sexual reproductive organs. However, small knots, each consisting of a few cells as in Text-Figs. 4 *a*, *b*, showed one internal binucleate cell, surrounded by a layer or two of growing uninucleate hyphal cells. This binucleate cell, representing primordial knot, distinguishes itself in having granular and more dense cytoplasm and also by giving deeper stain reactions as compared to the vacuolated and lighter stained surrounding cells.

Later stages of the cleistothecium maintain this distinction (reaction to stain) from which it is evident that the ascogenous system is formed from the deeply stained initial binucleate cell, while the cleistothecial wall is formed from the uninucleate light cells, surrounding it.

A number of slides of such primordial knots, cut through their various planes, were examined where it was revealed that the deep staining binucleate cell is a solitary one. Detailed examination was carried out to study whether there occurred any other cells in the vicinity of this binucleate cell which showed the same staining reactions; if it does, then whether the nuclear migration occurs from this to the central cell, resulting in the primary dikaryotic cell. No such conditions were found in this work. The origin of the dikaryotic condition, therefore, is the result of the division of a nucleus of the deep staining cell. Occasionally, a difference in sizes of the two nuclei in the binucleate cell—one definitely larger than the other—is noticeable (Text-Fig. 5).

Study and finding out of the actual development of the ascogenous hyphae from the initial binucleate cell has not been possible to follow as, indeed, they grow and branch too rapidly and also their overlapping and interweaving nature makes it difficult to trace their connections. They fill the central part of the cleistothecium, and are distinguishable as stated previously by their dense cytoplasmic contents. The cells of the hyphae are all uninucleate at this stage. Soon a change is

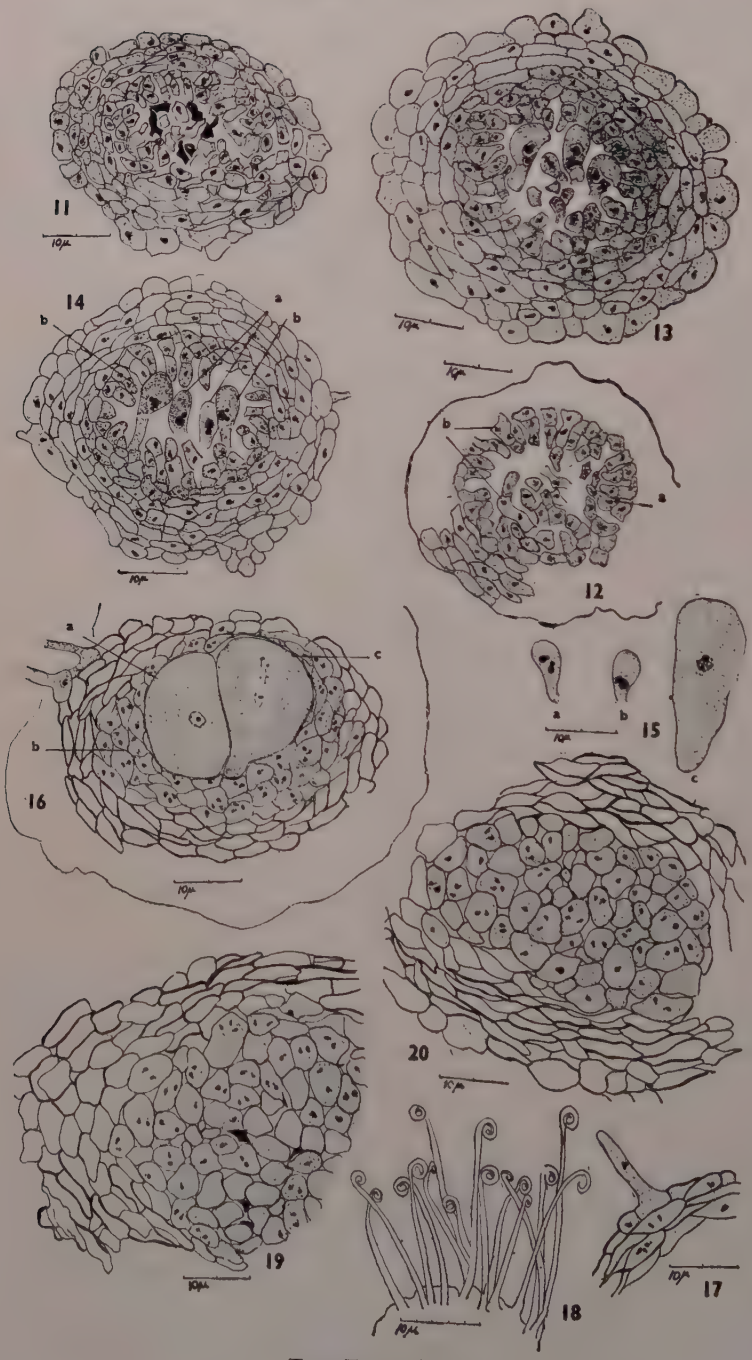
observed in the behaviour of the cells in the centre of the cleistothecium. They begin to disintegrate, shrivel and die (Text-Fig. 11).

This degeneration of the central cells makes enough room for the ascogenous hyphae to grow inwardly in radial rows each of two to four cells. A section of the cleistothecium at this stage clearly indicates the peripheral concentric arrangement of the sheath cells and the central radial rows of the ascogenous hyphae (Text-Fig. 12). These ascogenous hyphae growing centripetally and set in radial rows are mostly uninucleate with a few exceptions where either the terminal (Text-Fig. 12 *a*) or the penultimate (Text-Fig. 12 *b*) cells show a binucleate condition.

Although all these binucleate cells, penultimate or terminal, are potential ascus initials, asci develop from those arising from the cells at the floor of the cleistothecium (Text-Fig. 13). Text-Figures 13 and 15 *a* show the young binucleate ascus. Each nucleus has a distinct nucleole and a mass of irregularly twisted chromatin. The fusion of two such nuclei occurs when the ascus is still a young structure. The pairing nuclei lie closely in the centre of the slightly bulged ascus. The nuclei are drawn towards each other, lying sideways. The adjacent membranes are absorbed and the contents flow together. The nucleoli fuse last after the fusion of the components of their chromatin masses (Text-Fig. 14). The fusion nucleus is almost twice the size of the individual nuclei that went into fusion (Text-Figs. 14 *a*, 15 *b*). This product of fusion within the ascus, as the definitive nucleus, has been found to persist over quite a long period before it undergoes any further changes, thus providing a required period of rest and maturation till the ascus in which it lies (Text-Fig. 15 *b*) attains a larger size (Text-Figs. 15 *c*, 16 *a*). Text-Figure 10 shows the comparative sizes of asci with the nucleus within. The asci growing vertically in the centre attain larger size as compared to those arising from the sides. The asci occurring from two to ten in each cleistothecium, six to eight being more common, are more or less fusiform and at the broader region measure 36–43 μ and 67–83 μ in their height.

The whole of the cleistothecium after nuclear fusions in the asci consists of five to six-layered peridium of brown, thick-walled and flattened cells with the central group of asci. Surrounding these asci and immediately inside the projecting sheath is a distinct layer or two of uni-, bi- and trinucleate cells (more commonly binucleate) representing the "nurse cells" (Text-Fig. 16 *b*).

The cleistothecium at this stage begins to put forth the appendages. Cells in the outer layer of the peridium which have maintained thin walls, develop protuberances radially (Text-Fig. 17) which constitute the unbranched, unicellular and uncinate appendages (Text-Fig. 18). They are seen growing all over the cleistothecium except on its basal side. The other cells of the wall layers of the cleistothecium further develop pronounced thickening, giving the necessary firmness to the resting cleistothecial body and protection to the delicate internal structure,



TEXT-FIGS. 11–20

TEXT-FIGS. 11–20. Fig. 11. Degenerating central cells in cleistothecium. Fig. 12. Central radial rows of ascogenous hyphae with layers of peridium. *a*, terminal binucleate cell; *b*, penultimate binucleate cell. Fig. 13. Young binucleate ascus. Fig. 14. Karyogamy in the ascus. *a*, fused nucleus; *b*, fusing nuclei. Fig. 15. Comparative sizes of growing asci accompanied by nuclear changes within. *a*, binucleate ascus; *b*, ascus with the definitive nucleus; *c*, ascus with the definitive nucleus grown in size. Fig. 16. *a*, Ascus with definitive nucleus; *b*, nurse cells surrounding the asci; *c*, anaphase of the first division of the fusion nucleus. Fig 17. An appendage of cleistothecium in early development. Fig. 18. Uncinate appendages when mature. Fig. 19. Radial section passing through the "sterile cleistothecial" body showing pseudoparenchyma enclosed in by thick-walled cells. Fig. 20. Tangential section of the same body showing a similar structure.

As the cleistothecial wall develops, notable nuclear changes occur in the maturing asci. This is well represented in Text-Fig. 6 drawn to one scale, showing the comparative sizes of the nuclear pair to start with and then the fused product passing through various phases till the definitive nucleus attains its maximum size prior to division. The enlarged nucleus (Text-Fig. 6) shows chromatin material spread out to form a reticulum—the spireme stage of the first division. The chromatin material then contracts considerably and collects in a mass leaving a large vacant nuclear area (Text-Fig. 7). This is the synaptic phase preparatory to meiosis.

First division of the fusion nucleus of the ascus has been clearly recorded in its metaphase (Text-Fig. 8) and anaphase (Text-Fig. 16 *c*). The spindle of this division always lies parallel to the longer axis of the ascus. The spindle does not restrict itself to the nuclear membrane but stretches far beyond it. The nucleole which is quite distinct at the beginning of the nuclear division degenerates later. The metaphase shows four units of chromosomes (chromatin blobs) and the anaphase also depicts four chromosomal bodies departing towards each of the two opposite spindle poles. This first division of the fusion nucleus showing the synaptic phase is meiosis. Of the four chromosome units, seen in the metaphase, each is a bivalent chromosome structure. The two component chromosomes of each pair are derived from the two nuclei that have fused within the ascus; while the eight chromosome bodies at the anaphase—four going to the two respective poles—are the eight chromosomes after their segregation from the four bivalents. On reaching the poles of the spindle each group of (four) chromosomes forms spireme and the nucleole and the nuclear membrane appear. Thus two daughter nuclei after the first division are visible at two opposite poles in the ascus (Text-Fig. 9).

These nuclei move quite apart, and increase in size (Text-Fig. 10) previous to the second division. There is no definiteness regarding the orientation of the two spindles of the second nuclear division in the ascus.

The two spindles seen in metaphase (Text-Figs. 21, 22) belong to the same ascus occurring in its two consecutive sections. In both, four chromosomes are visible. Text-Figure 23 shows the late anaphase of the second division where a group of four chromosomes can be made out at each of the poles. This second nuclear division is equational

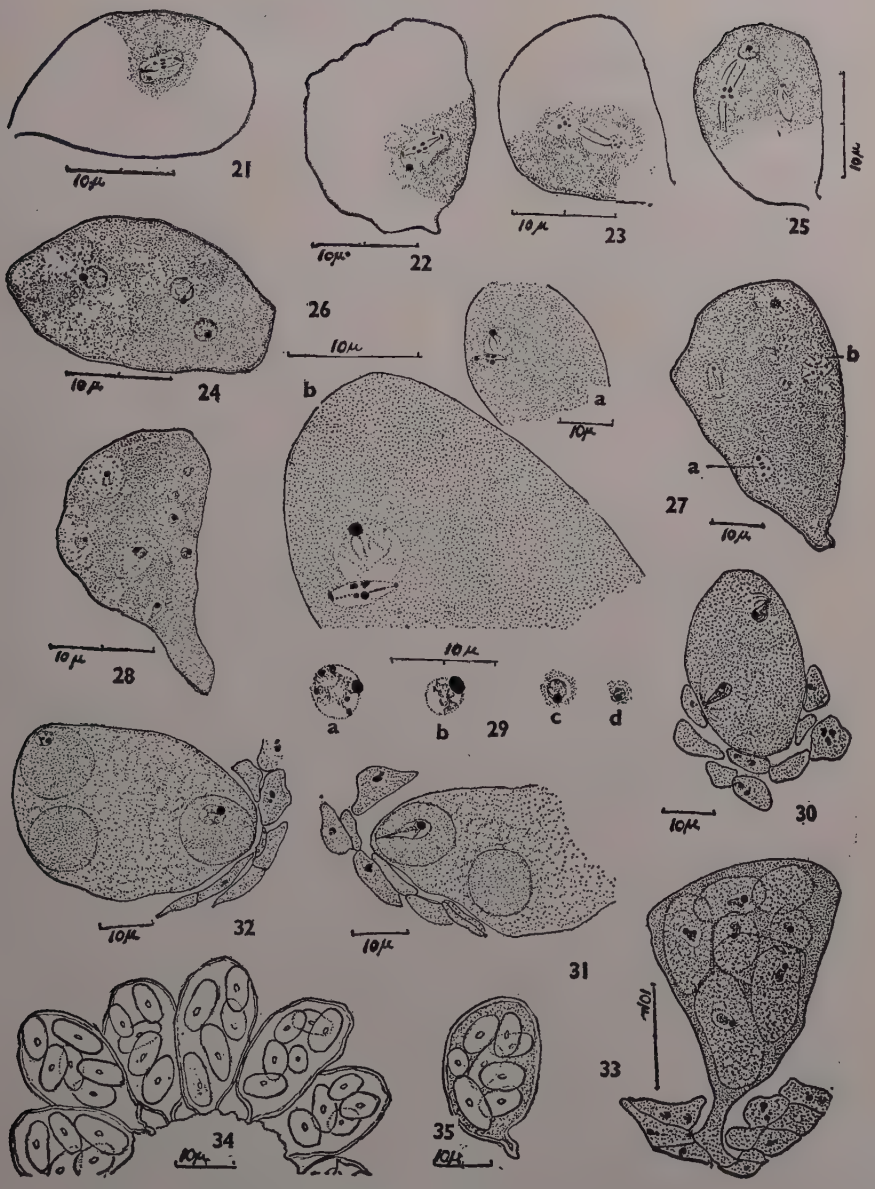
forming four well-organized daughter nuclei. Text-Figure 22 shows three and the fourth nucleus is in the next section.

Text-Figures 25 and 26 show the metaphase of the third division with four chromosomes at the equator. Not only were all the spindles not present in one and the same section but all the nuclei did not enter into a simultaneous division. Some of the nuclei are seen far ahead in their phases of division, while others do not show yet a sign of the prophase. Text-Figure 27 shows both at '*a*' and '*b*' a group of four chromosomes at the spindle poles, belonging to two different spindles. This is the late anaphase of the third division of the fusion nucleus which is mitotic like that of the second one. This results in the formation of eight nuclei (Text-Fig. 28) where six are very clear and the remaining two are made out by two dark spots through which the section has passed. It has been noted that with the successive divisions, the nuclear and chromosomal size reduces appreciably. Text-Figure 29 depicts the three nuclei prior to their divisions where '*a*' shows the fusion nucleus, '*b*' the daughter nucleus of the first division, '*c*' daughter nucleus of the second division and lastly '*d*' the ascospore nucleus. Chromosomal size-decrease can be seen in the figures of the three divisions.

These observations indicate that in *U. tectonae* the first division of the fusion nucleus is reductional, the successive two are equational; haploid chromosome number is four, and diploid is eight.

After the formation of eight nuclei, development proceeds in the ascus to complete the ascospore formation. At each one of the eight poles, the nucleus is beaked and its pointed end lies at the pole from which the astral rays are seen radiating (Text-Fig. 30). Spore formation in *U. tectonae* follows the same usual pattern of Erysiphaceae in delimiting a portion of the cytoplasm surrounding the nuclei by following the line of the astral rays. Further advance in spore development is seen in Text-Fig. 31. This beak is soon lost and the nucleus moves in the centre of the ascospore which appears more or less rounded (Text-Fig. 32). Such nuclei that do not further develop into ascospores are found degenerating. The ascospores grow in size and from their early round shape, change to elliptical at maturity (Text-Fig. 33). Their usual number in *U. tectonae* is from four to six (Text-Fig. 34), though eight is not rare (Text-Fig. 35). They measure $23–27 \times 12–13\,\mu$.

While studying sectioned material of cleistothecia in *U. tectonae* quite an unexpected feature was revealed in the present investigation. A large number of cleistothecial bodies, measuring $130–200 \times 80–150\,\mu$ and showing a distinct peridium consisting of almost empty, thick-walled cells, encasing a mass of isodiametric cells—the pseudoparenchyma —have been noted. The cells of the stroma are thin-walled, full of granular cytoplasm and are bi- or trinucleate. Though not typically flattened like the nourishing cells of the fertile cleistothecia, these cells do resemble the former in being full of cytoplasm, bi- or trinucleate and in their staining reaction. Such 'cleistothecial bodies' do not show the normal development of appendages, in that, either there is



TEXT-FIGS. 21–35. Figs. 21 and 22. Metaphase of the second nuclear division in the ascus in consecutive sections, showing 4 chromosomes at the equatorial plate. Fig. 23. Anaphase of second division with groups of four chromosomes at each of the two spindle poles. Fig. 24. Three out of the four daughter nuclei resulting from the second division in the ascus. They are again well formed. Figs. 25 and 26. Third nuclear division in metaphase with four chromosomes; also shows other nuclei which have not yet set into division. Fig. 24 '*b*' is magnification of Fig.

24 '*a*'. Fig. 27. Anaphase of the third nuclear division showing four chromosomes at the poles of two different spindles *a* and *b*. Fig. 28. Products of the third nuclear division forming eight nuclei out of which six are clearly represented. Fig. 29. Comparative sizes of the nuclei prior to their divisions in ascus. '*a*', before first division; '*b*', before second division; '*c*', before third division; '*d*', ascospore nucleus. Figs. 30–33. Successive stages in ascospore formation. Fig. 34. 4–6 ascospores in each of the asci. Fig. 35. 8 ascospores in an ascus.

a complete lack of their development or when present, they are very few.

Thorough search was made of the serial sections of these bodies to find whether any asci were developed within them. Text-Figure 19 shows a radial section and Text-Fig. 20 a tangential section of such cleistothecia. The most striking feature of these bodies is the complete absence of asci within them; when other cleistothecia even smaller in size have always shown their fertile nature through their contents (asci).

In Ascomycetes, the initiation of the ascocarp peridium formation is supposed to be the effect of the stimulation of sex or that of strain-plasmogamy, or at any rate that of the apogamous establishment of the dikaryon within the ascogenous system; later culminating in the development of the asci. In the present work, it has been found that some young (small in size) and mature (larger in size) "Cleistothecia" showed no traces of asci, though externally they resemble the fruit bodies of *U. tectonae*. They have thus been formed of completely sterile hyphae, and for all considerations, therefore, are not initiated with sexual impetus. The inference, therefore, is that such bodies in *U. tectonae* are equivalent to the sclerotia occurring in other Ascomycetes. They function likewise to tide over the unfavourable conditions (period of summer in the life-cycle of *U. tectonae*) and sprout out in vegetative growth on the advent of favourable condition in the following season.

Comparison and Discussion

For convenience and easy reference, the findings in this work of *U. tectonae* have been compared (I) with the other species of *Uncinula* and (II) with the other species in the genera of Erysiphaceae.

I. No cytological work has been noticed, on any of the Indian species of *Uncinula* (*U. salicis*, *U. polychaeta*, *U. necator* and *U. tectonae*) so far, and such work done abroad, as was available, is found in the following papers: on *U. clandestina* by Eftimiu (1929); on *U. clandestina* and *U. spiralis* by Raymond (1934); on *U. aceris* and *U. salicis* by Eftimiu and Kharbush (1928).

It is interesting to note that *U. tectonae* (*a*) shows certain similarities with the above-mentioned species of *Uncinula*: (1) absence of nuclear migration; (2) from the available information on the point of the origin of the dikaryon it appears to be consistently apogamous; (3) karyogamy occurs only in the ascus and not in the ascogonium; (4) number of ascospores in the ascus is 4–6; (5) the chromosome count in the other species of *Uncinula* (*U. clandestina* and *U. spiralis*)

TABLE I

Parasite	Conidiophore	Conidia	No. of asci	Ascus	Cleistothecium	Appendages	Ascospores	Host
U. necator (Stevens) 1925	Short	Elliptic oblong or obtusely rounded, hyaline 25–30 × 15–17 μ	4–6 rarely 9	Ovate-oblong to subglobose with or without stalk 50–60 × 30–40 μ	70–128 μ	7–32 rarely 40 1–4 times the diameter of the cleistothecium	4–7 18–25 × 10–12 μ	*Vitis Ampelopsis Actinidia*
U. necator (Butler & Jones) 1949	Erect, short	Oval, hyaline 25–30 × 15–17 μ	2–8	Ovoid 48–60 × 37–45 μ	75–105 μ	8–25	6 20 × 13 μ	*Vitis*
U. tectonae (Salmon) 1900	Erect, end abstricting Conidia measure 7·5–9 μ	Oblong, hyaline 37–40 × 13–17 μ	2–10 usually 6–8	Broadly ovate, 67–83 × 36–43 μ	120–123 × 140–160 μ	20–60 or a little over 83–133 μ in length	4–8 more often 6 23–27 × 12–13 μ	*Tectona grandis*

recorded, concurs with that of *U. tectonae* 4 haploid and 8 diploid; (6) although no specific mention has been made regarding the occurrence or otherwise of brachymeiosis, it could be inferred that in these species, like *U. tectonae* brachymeiosis does not exist; (*b*) shows the following differences with the rest; (1) there are no distinct sexual reproductive organs in *U. tectonae*.

In the absence of other information on the morphology of the *Uncinula* species cited above no comparison could be made in this connection. From the *Uncinula* species, morphological data could be collected from previous work only for *U. necator* (Schw.) Burr. (Stevens, 1925). A comparison on these points has been made with the findings on *U. tectonae*, and listed in Table I.

II. Detailed historical account of the investigations on the other species from Erysiphaceæ appears in recent works of Olive (1953) and Tare (1955). Observations made in the present study are compared with the previous findings on Erysiphaceae.

Completely diverse views are put forward on features occurring in the life-histories of Erysiphaceae; and therefore, the task of comparison would be too long drawn out. Hence, significantly important points—such as presence or otherwise of sexual bodies; if present, whether functional or not; the derivation of the two nuclei in the dikaryotic initial; the ascus development and the nuclear divisions in ascus with chromosome counts—are considered here.

From Wentzel's (1929) report, early workers like Harper (1896, 1905) working on *Erysiphe communis*, *Phyllactinia corylea* and *Sphaerotheca castagnei*, Blackman and Fraser (1905) on *Sphaerotheca humuli* and Wentzel (1929) on *Erysiphe aggregata* have recorded the development of an ascogonium and an antheridium. Also in the other genera of Erysiphaceae, as referred to by Olive (1935), *Sphaerotheca* and *Podosphaera* [Eftimiu and Kharbush (1928), Kharbush and Eftimiu (1928), and Eftimiu (1929)], *Microsphaera* (Raymond, 1933); and in case of *Phyllactinia corylea* Colson (1938), *Erysiphe* (amongst others, Tare, 1955)—such sexual bodies have been described. *U. tectonae* does not possess sexual reproductive organs.

Harper (1896, 1905) and Blackman and Fraser (1905) describe both ascogonium and the antheridium to be convincingly functional having seen the passage of a nucleus from the antheridium to the ascogonium. However, working on the same fungi Dangeard (Swingle, 1934) on *Sphaerotheca castagnei* and de Bary (Wentzel, 1929) on *S. humuli* have described the antheridium as non-functional and this again has been confirmed by Winge (Gwynne—Vaughan, 1922) for *S. castagnei*. As late as 1934 (Homma), 1941 (Bergman) (quoted from Olive, 1953), researches on *Sphaerotheca fulginea* and on a related species of *S. castagnei* respectively, have brought out the affirmative evidence of the migration of the antheridial nucleus to the ascogonium. Tare (1955) deduces inferentially the antheridium to be functional. though no direct migration was observed.

It is interesting to note, however, that Kharbush and Eftimiu (see Olive, 1953) who reworked some of the species of the powdery mildews previously studied by Harper have concluded that the antheridium is non-functional resulting in the absence of plasmogamy where it was previously stated to occur. A non-functional antheridium and, therefore, absence of plasmogamy are the observations as recorded by Olive, 1953, of Moreau and Moreau (1930) on *S. castagnei*, of Raymond (1938) on *Microsphaera quercina*; while Colson (1938) on *Phyllactinia corylea* observes that the antheridium is not only functionless but it also degenerates.

Allen's (1936) observations on *E. polygoni* are, "in sexual reproduction hyphae swell towards each other or communication may be established at the joined apices of two hyphae or between short side branches on adjoining hyphae. The opening between the two fusing cells broadens rapidly. No indication has been seen that nuclear fusion occurs in the fusion cells". Also in her work on *E. cichorocearum* (quoted from Tare, 1955) she has observed the same attraction between hyphae at the beginning of sexual reproduction. Broad areas of contact were established between hyphae and the passage of a nucleus from one hyphae to the other seemed quite common; such fertilisation was achieved without the formation of specialised reproductive branches and she is emphatic in saying that nothing in this case could be labelled as "antheridial" or "oogonial" branch.

From the above considerations it would be possible to draw a general sequence in the organisation of sexual organs in Ascomycetes as:—

(*a*) Definite sexual organs present and functional.

(*b*) Definite sexual organs present but antheridium non-functional.

(*c*) Definite sexual organs present but antheridium sterile and degenerating.

(*d*) Definite sexual organs not present but fusion of vegetative hyphae occurs prior to the establishment of binucleate "ascogonium".

(*e*) Definite sexual organs not present and no fusion of vegetative hyphae.

As stated earlier, *U. tectonae* presents a case of the last category and further no fusion occurs in vegetative hyphae resulting in plasmogamy.

Observations in *U. tectonae*, regarding the apogamous development of the dikaryon in the absence of plasmogamy, are in agreement with the findings in the other genera, namely, *Podosphaera*, *Sphaerotheca*, *Microsphaera* and *Phyllactinia*. In *Podosphaera* and *Phyllactinia* the ascogonial nucleus divides mitotically several times resulting in a row of cells one amongst these being binucleate and the rest uninucleate. Colson (1938) is of the opinion that the apogamous development of the ascogonium in *P. corylea* is by the division of its nucleus resulting in two different-sized nuclei in the ascogonium; however, the actual division she has not been able to note. In *U. tectonae*, therefore, in the absence of plasmogamy it has to be assumed in line with Colson's contention that the origin of the two nuclei in the binucleate initial cell must be the result of the division of its original nucleus. These two nuclei showed no particular size difference except rarely. Bergman (1941) (quoted from Olive, 1953) found in *S. castagnei* the pair of sexual nuclei (after plasmogamy) to be morphologically different due to their size difference (one larger than the other) during their pairing in the oogonium.

In *U. tectonae* no nuclear fusion has been observed in the initial binucleate cell. All recent workers (within the last 30 years) except Homma (1934) (from Olive, 1953), (who describes the actual fusion of the antheridial and ascogonial nuclei) unanimously observe no nuclear fusions prior to the one in the ascus.

Regarding the successive developmental stages of the ascogenous hyphae there seems a common difficulty experienced by most of the workers in their investigations on forms of this group, as is well expressed by Gaumann and Dodge in their *Comparative Morphology of Fungi* (1928), "the relationships are difficult to follow cytologically as the copulation branches are already surrounded by a thick hyphal

knot into which the primary ascogenous hyphae, growing out from the ascogonium, penetrate with irregular twistings". In the present investigation also when these intermediary stages of development of the ascogenous hyphae were involved, the same was acutely experienced on account of the fast growing, branching and intertwining nature of the hyphae and the absence of any morphological distinction between sexual apparatus and the vegetative fungal hyphae. The " ascogonium " is only discernible on account of its binucleate condition at early developmental stages of the cleistothecium. So that in sections and in the whole mounts it proved quite a difficult task to correlate the connections of one with the other. In the initial developmental stages of the binucleate cell, differing structures have been observed by workers after the mitotic divisions of the ascogonial nuclei, varying from the normal to an ununiform septation resulting for some time in a cœnocytic condition. Colson (1938) gives more definite serial phases of this development. She states that after the mitotic divisions, the ascogonium becomes three-celled, the middle being binucleate from which arise the ascogenous hyphae. They are multinucleate at first and then septate so that rows of binucleate cells are formed with a uninucleate cell at the top and base of every row. No such regular arrangement was noted in *U. tectonae* as also in *E. acaciae* by Tare (1955) who reasons it as due to " the intricate arrangement of the developing hyphae".

In connection with the ascus development a general observation is that the penultimate binucleate cell of the ascogonial hypha develops into an ascus. In *U. tectonae* the ascus formation is not strictly restricted to the penultimate binucleate cell, but terminal binucleate cells have also been found to develop into asci.

The process of divisions of the fusion nucleus in the ascus of *U. tectonae* shows similarity to that found in *P. coylea* (Colson, 1938) and in *E. acaciae* (Tare, 1955). Text-Figure 15 shows the fusion nucleus in one of the preparatory stages of the nuclear division—the synapsis; clearly marking out this first division of the fusion nucleus in the ascus to be the meiotic one. At the metaphase of the first division, four bivalents (*i.e.*, homologous pairs) are seen at the equatorial plate and as the division proceeds to the anaphase, a group of four univalents gather at each of the spindle poles (or in other words, the two components of each of the four chromosomal bodies seen at the metaphase of the first division of the nucleus in the ascus are derived from the two fusing nuclei). In the first division, therefore, the number of chromosomes is reduced from 8 to 4. This first division is heterotypic. This is followed by the second division of the daughter nuclei where at metaphase again, 4 chromosomes are made out. They split individually—the two halves of each chromosome separate to form a group of 4 at the respective poles. Same happens during the third division. These last two divisions are homotypic. From the description of all the three divisions, it is clear that the first division in the ascus is the only reductional followed by two homotypic divisions. Therefore, like *S. castagnei* and *P. corylea* (Eftimiu and Kharbush, 1928) as quoted by Olive (1950), *P. corylea* (Colson, 1938) and *E. acaciae* (Tare, 1955) in the life-

history of *U. tectonae* there is only one fusion, which occurs, only one reductional division and hence no brachymeiosis. The haploid number of chromosomes in the above three species is 10, 4 and 4 respectively.

Summary

In the study of the morphology, development and cytology of *U. tectonae* (Salmon) occurring on *T. grandis* (L.) the following has been noted:—

(1) Measurements: hyphae 3 μ; conidiophores at the base 4·5–6 μ and at the apex 7·5–9 μ; conidia oblong, 37–40 $\times$ 13–17 μ; cleistothecia globose to sub-globose, 120–23 $\times$ 140–60 μ; asci broadly ovate, 67–83 $\times$ 36–43 μ and ascospores oblong, ends obtuse, 23–27 $\times$ 12–13 μ.

(2) Germination of conidia was observed. Climatic conditions such as hot days changing to cold nights, specially favour both conidial germination and growth of the fungus.

(3) Sexual reproductive organs are lacking.

(4) In the detailed examination during this investigation nuclear migrations have never been observed.

(5) The dikaryon is developed apogamously by division of the original nucleus.

(6) The developmental stages of the cleistothecium culminating in the formation of the ascus were studied—either the terminal or the penultimate binucleate cell of the ascogenous hypha develops into the ascus.

(7) Karyogamy in the ascus and the successive three divisions of the definitive nucleus have been noted. The first division is the reducing division; wherein there are four homologous pairs of the chromosomes in the ascus nucleus and four chromosomes pass to each spindle pole. The following two divisions are equational and the same four chromosome number is maintained in them. The diploid number of chromosomes is therefore 8 and the haploid number is 4.

(8) Ascospore formation has been followed. Usually 4–6 ascospores occur in an ascus.

(9) A very unusual formation is recorded in *U. tectonae*. Large cleistothecium-like bodies with a few or no appendages have been observed. Externally they more or less resemble the fertile cleistothecia, but internally they are devoid of any asci. Inside the brown thick-walled sheath the whole space is filled with isodiametric pseudoparenchyma, whose cells are full of cytoplasm and are bi- or trinucleate. Such a "cleistothecial" body is hence described as "sclerotium", over-summering, later to grow vegetatively with the advent of favourable conditions. As compared to the normally

globose cleistothecium, these bodies are horizontally elliptical. They measure 80–150 × 130–200 μ.

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MORPHOLOGY OF TWO INDIAN SPECIES OF *BOLBITIS*

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Bolbitis Schott. is a much confused genus of tropical ferns with *c.* 85 known spp. distributed mainly in the Indo-Malayan region. The morphology of the genus is little known and its affinities are still a matter of opinion. The different spp. that now constitute *Bolbitis*, especially the Oriental ones, were much confused with such unrelated genera like *Leptochilus* and *Campium*. The present discussion deals with the morphology of two little known Indian spp., *viz.*, *Bolbitis* (*Acrostichum* Hook., *Campium* Presl., *Leptochilus* Rheede, *Paecilopteris* Moore, *Gymnopteris* Bedd.) *subcrenata* (Hk. *et* Grev.) Ching, and *B. virens* (Wall.) Ching. Copeland (1928) considers *Bolbitis* as of Polypodioid origin the nearest relative being "*Polypodium selliguea*". A short description of *B. subcrenata* is given by Hooker and Greville (1828) based on specimens from E. Ceylon, under the name *Acrostichum subcrenatum*. Later, in his *Species Filicum* Hooker reduced the species as a variety of *Acrostichum* (*Bolbitis*) *virens* Wall. In his *Synopsis Filicum* (1868) he recognises it as a variety of 'proliferum' distinguishable from true *A. virens* by its broader pinnæ, goniopteroid venation and the elongated bulbil-bearing terminal pinna. Beddome (1892) made vigorous objection to combining *subcrenata* with *virens*. He contends that *B. virens* is unknown in Southern India, occurring only in Sikkim, Burma, Siam, Penang, etc. Copeland (1928) recognises *B. subcrenata* as distinct from *B. virens*, but bases his observations on the descriptions of Beddome and on the lonely collection of Lawson from Cochin (S. India).

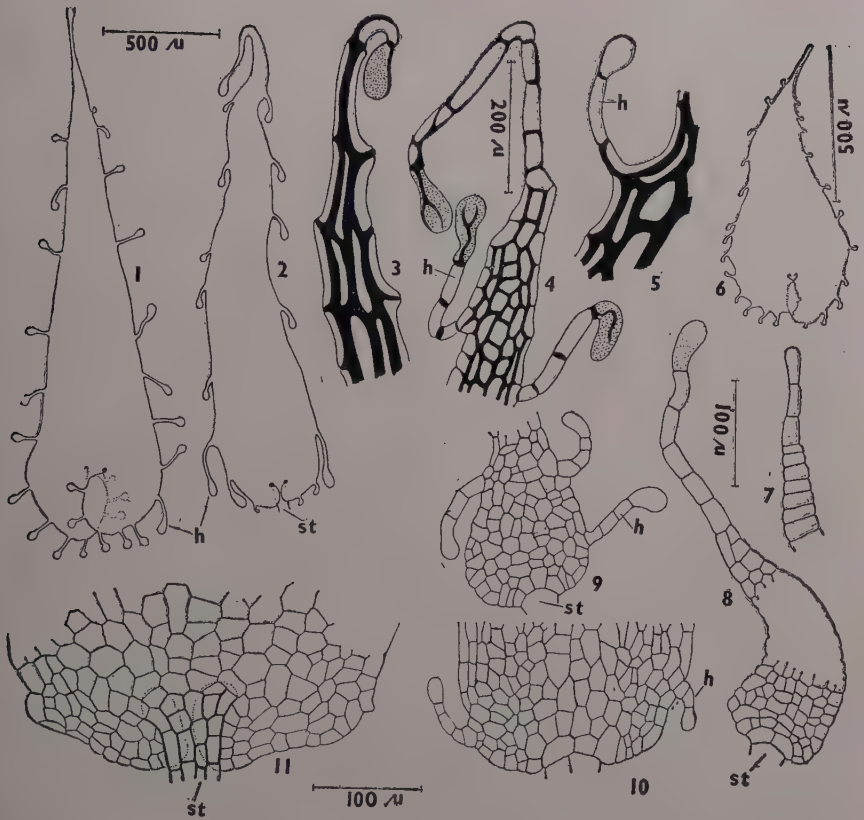
Little is known regarding the morphology of the sporophyte of any sp. of *Bolbitis* and almost nothing is known about the gametophytes. The present study was undertaken with an idea of describing the morphology of the two spp., so as to facilitate correct identification, and to assess the extent to which the morphology of the sporophyte and the gametophyte is useful in ascertaining the phylogeny of the genus.

Material for the present study was collected from the Western Ghats of South India (Coll. No. NBG 45533, *B. subcrenata* from Kanchenkumri, Hassan District, Mysore State; NBG 45559, same from Mercara, Coorg; and NBG 45058, *B. virens*, from Shabari Malai, Kottayam District, Kerala State. Herbarium sheets of these materials are deposited in the Herbarium of the National Botanic Gardens,

Lucknow). Material preserved in F.A.A. was used for anatomical studies, and free-hand sections stained with safranin and fast green were extensively used. Spores collected from plants growing wild at Shabari Malai, Mercara, Kanchenkumri and Agumbi (Western Ghats of South India) in March–April 1957 were sown in July 1957 for study of germination and prothallial morphology. All observations recorded here are based on these cultures. Spore cultures were made in special unglazed earthenware pots filled with well-deteriorated, sterilized moss and supplied with $\frac{1}{2}$ strength Knop's solution from below. Funnel-shaped earthenware pots nearly 10 cm. in diameter and with a hollow open pout at the bottom ("Chillum") were used for cultures. After sowing of spores the pots were kept in a specially designed germinating chamber. The chamber used is of simple design, having a rectangular cement tub, 1·2 m.×0·6 m.×0·2 m., with a perforated cement slab fitting on to ridges on the sides about 10 cm. below the rim. The perforations are 7 cm. in diam. and serve to hold the pots vertical with their pouts protruding downwards. The tub is filled with culture solution to the extent that the solution reaches up to the perforated slab and covers the bases of the culture pots. Constant supply of the requisite quantity of the solution to the cultures is accomplished by the capillary action of the wall of the pots. The culture solution is replaced every fortnight by draining off the old solution through a tap fitted on to the bottom of the tub. Protection to the cultures is afforded by a glass roof fitted to the top of the tub. The germinating chamber is kept in a well-illuminated cool place, away from direct sunlight. For study of early stages of prothallial development, floating cultures were raised in Petri-dishes, using $\frac{1}{4}$ strength Knop's solution.

Observations

Bolbitis subcrenata and *B. virens* grow mostly in shaded rocky areas, the former being far too common in the area where collections were made, than the latter. The rhizome is horizontally creeping, a centimetre or slightly more thick, 8–12 cm. long, brownish-black in colour, usually unbranched and with thick, wiry, black roots profusely on the undersurface. The leaves are two ranked, closely set, restricted to the upper surface and each associated with a dormant bud on the abaxial side (Text-Fig. 12) . One or two roots occur lateral to the bud and associated with it. Roots originate only from the undersurface (except those associated with buds) and are mostly in irregular transverse rows beneath each leaf base. The surface of the rhizome and leaf bases are covered by lanceolate paleae (Text-Figs. 1, 2) with a broad base and gradually tapering apex. They are blackish and clathrate with the side-walls of cells heavily thickened. The marginal cells are thin-walled and hyaline. The base of the palea is deeply cordate with the lateral lobes forming overlapping auricles which make the palea apparently appear peltate ("Pseudopeltate" condition). The auricles are prominent in *B. virens* in which all or nearly all paleae are distinctly pseudopeltate, while in *B. subcrenata* many paleae have cordate bases with non-overlapping basal lobes. Each palea terminates in an uniseriate



TEXT-FIGS. 1–11. Morphology of paleae. Fig. 1. Entire palea from rhizome of *Bolbitis virens*. Fig. 2. Same of *B. subcrenata*. Fig. 3. Apex of mature palea of *B. subcrenata*. Fig. 4. Apex of a young palea of same. Fig. 5. Marginal hair on mature palea of same. Fig. 6. Palea on stipe of *B. virens*. Figs. 7–11. Stages in the ontogeny of paleae of *B. subcrenata* (*h*, hair. *st*, stalk).

hair with thickened cross-walls and topped by a swollen club-shaped cell with dense brown contents, probably glandular and tannin-containing (Text-Figs. 3, 4). Similar but smaller multicellular uniseriate hairs occur profusely all over the margin (Text-Figs. 4, 5). Some of these hairs lack thickenings of cross-walls and the dense contents of the terminal cell. The incidence of marginal hairs is more on the auricles where, in some cases, almost every marginal cell bears a hair and some of the hairs may remain unicellular with a club-shaped apex. The hairs are shorter in *B. virens*, most of them being two cell long. Paleae covering the leaf-bases and stipes tend to be ovate-lanceolate (Text-Fig. 6) and progressively smaller up the stipe. Each palea originates as a stout multicellular uniseriate hair with barrel-shaped basal cells and a tapering apex. The hair becomes 10–12 cells long with the upper cells progressively longer (Text-Fig. 7). The terminal cell soon

enlarges and acquires dense contents, which ultimately turn deep brown. The transverse walls of the posterior cells below the terminal cell become thickened and gradually turn brown. Longitudinal divisions of the other cells (except the basal one) initiate flattening of palea (Text-Fig. 8). The basal cell remains undivided and forms the stalk. The frequency of divisions is more in cells near the stalk cell, decreasing progressively towards the apex, resulting in a lanceolate palea (Text-Fig. 9). The base becomes cordate and the lobes expand by diffused growth, there being no definite meristematic region (Text-Fig. 10). The stalk cell divides to form a short broad stalk, 2 or 3 cells thick and 3 to 6 cells broad (Text-Figs. 10, 11, *st.*). Marginal hairs are developed on young paleae after the development of the cordate base (Text-Figs. 9, 10, *h.*). Hairs are developed first towards the apical region and gradually extend downwards. The clathrate thickening of the palea cells initiates towards the apex of the paleae and gradually spreads downward till it reaches the stalk, which remains comparatively thin-walled throughout.

The rhizome is fleshy with a thin-walled epidermis bearing paleae and a hypodermal sheath of comparatively thin-walled sclerenchyma (3–5 cells thick). The ground tissue is parenchymatous but a few cells towards the centre may develop brown contents in older regions of the rhizome. Groups of 2–5 cells scattered in the ground tissue have tannin deposits and give a mottled appearance to the sections of the rhizome. Such tannin cells occur in the ground tissue of the stipe also.

The adult rhizome has a solenostelic stelar cylinder (Text-Figs. 13, 15) with two rows of very prominent overlapping leaf gaps on the dorsal surface. The ventral half of the stele is entire and shallowly gutter-shaped or even band-shaped (Text-Fig. 13, *v.*). The leaf gaps are alternating and so closely placed that the dorsal region of the stele appears like a small vascular strand (Text-Fig. 13, *d.*) which fuses with either margin of the ventral gutter-shaped region alternately and is mainly concerned with the formation of leaf traces. A transverse section of the stele shows a broad ventral merisele (Text-Fig. 15, *v.*) and a small dorsal one separated from each other by a leaf gap on either side. Traces to each leaf number 8 to 10 in *B. subcrenata* and 5 to 8 in *B. virens*. The leaf gaps are broadly spindle-shaped and the traces for each leaf originate from both the margins though majority of the traces originate from the margin nearest the dorsal median line of the stelar cylinder. The basalmost trace, originating from the dorsal side of the gap, gives off a branch trace (Text-Fig. 13, *br.*) at its base. Each branch trace gives off a root trace towards its base and curves off sharply through the cortex of the rhizome to enter the bud associated with the leaf. The last two traces to every leaf (one from either margin of the leaf gap) are more prominent than the rest and constitute the prominent adaxial pair of bundles of the stipe. The traces constituting the vascular connection to each leaf establish interconnecting vascular commissures. Root traces are restricted to the broad intact ventral band of the stelar cylinder, the dorsal half of the rhizome being free of them, except for the solitary root traces associated with

TEXT-FIGS. 12–16. (*a*, lateral ridge, *b*, lateral bud, *br.* vascular trace to lateral bud; *d*, dorsal meristele; *l*, leaf base; *lg.*, leaf gap, *lt.*, leaf trace bundles; *p.*, vascular bundles to pinna; *r*, root trace; *rt.*, root.) Fig. 12. Apical end of entire rhizome of *B. subcrenata* (dorsal view). Fig. 13. Vascular structure of a portion of same. Fig. 14. T.s. stalk of pinna of *B. virens* showing two vascular strands. Fig. 15. T.s. rhizome of *B. subscrenata* (all traces marked l_1 supply one leaf while those marked l_2 supply the next one). Fig. 16. T.s. apex of stipe of *B. virens* showing departure of traces of pinna.

each bud. Mostly, roots originate opposite the region of departure of vascular connection to leaves.

Very young rhizomes are protostelic, the first few leaves having a single trace each. Later formed leaves have two traces per leaf, the traces originating one in front of the other in close succession from the dorsal surface of the stele. Further up the rhizome the two traces to each leaf originate one lateral to the other though one of the traces precedes the other. The stelar cylinder becomes grooved on the dorsal surface in such a way that the two traces for each leaf comes on either side of the groove. As the girth of the rhizome increases, the dorsal groove of the stelar cylinder becomes more and more pronounced till the stele becomes gutter-shaped. Vascular connection to each leaf is then established by two or three pairs of traces originating alternatively from either margin. The transition to the adult form is quite sudden and takes place by the formation of a dorsal vascular strand, which originates as a branch from one of the margins of the gutter-shaped stele immediately after formation of a leaf trace, or as a pair of branches, one from either margin, which fuse together soon. The dorsal strand thus produced fuses with the margin of the gutter-shaped ventral region producing the first leaf gap.

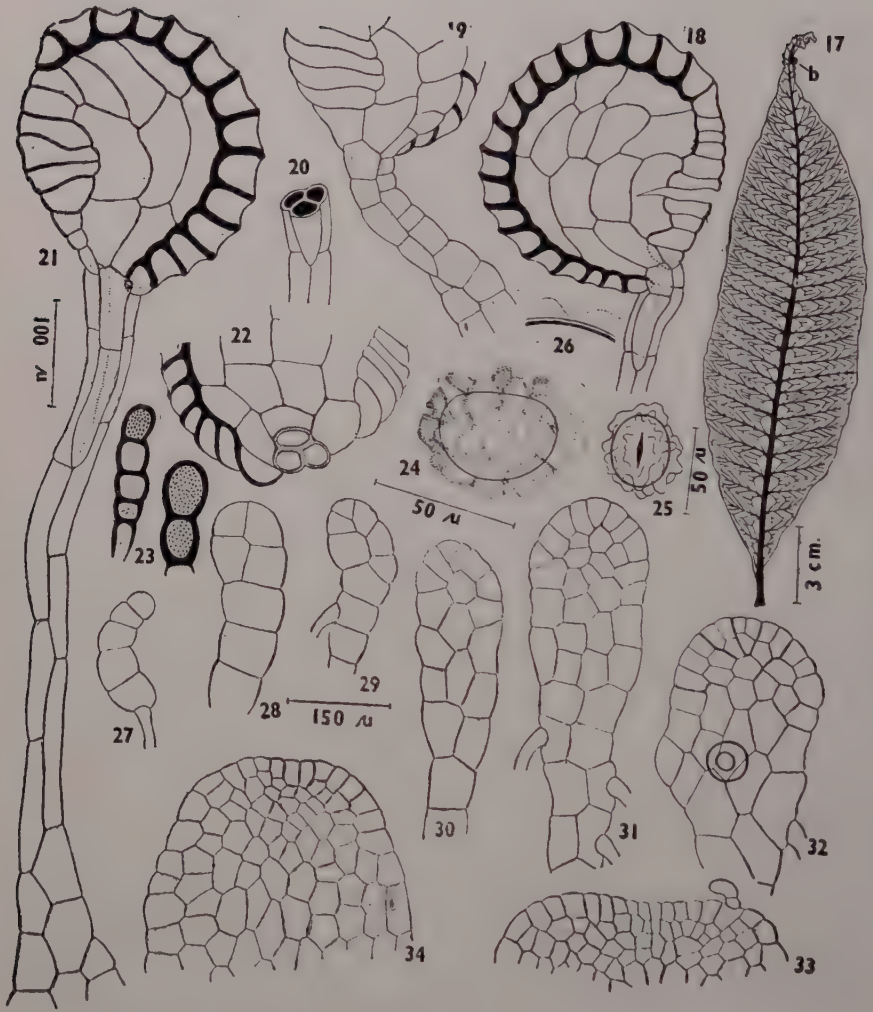
Leaves are in two alternate rows on the upper surface of the rhizome, are nonarticulated and closely set. In both the spp. they are pinnate with alternate to subopposite stalked pinnæ articulated to the rachis. Pinnae are 5–6 pairs in *B. subcrenata* and 7–9 pairs in *B. virens*. The stipe in *B. subcrenata* is up to 50 cm. long, pale green in colour, and has a swollen basal region where it joins the rhizome, the swelling in some of the larger leaves being *ca.* 1·0 cm. or slightly more in girth (Text-Fig. 12). The swollen part of the stipe is generally adpressed to the rhizome. The stipe in *B. virens* is up to 45 cm. long and is brownish tinged or may have a pale-violet hue. The swelling at the base of the stipe is not very prominent. Laterally on the swelling in both spp. are two prominent wedge-shaped ridges running longitudinally near the adaxial surface. These ridges (Text-Fig. 12, *a*.) continue all the way up the stipe, midrib and the stalks of the pinnae and are continuous with the lamina. The ridges are more prominent towards the base, are of a paler hue than the rest of the stipe and are less marked in *B. virens* than in *B. subcrenata*. The basal region of the stipe above the swelling is almost cylindrical, but the adaxial surface becomes flattened at first and later becomes grooved above. Further up, the groove splits into two, leaving a narrow ridge in the middle. The stipe is roughly four-angled towards the apex.

The swollen basal region of the stipe is parenchymatous, the ridges being composed of aerenchyma (loose parenchyma with prominent air-spaces). Further up the stipe and in the rachis there is a clear band of hypodermal sclerenchyma, 5–10 cells thick, highly thick-walled and pale brown in colour. At the region of the ridges a patch of aerenchyma interrupts the sclerenchyma sheath, thus connecting the aerenchyma of the ridges with the ground tissue. The stipe has many vascular bundles

arranged in a circle which is incomplete on the adaxial side. The two bundles on the adaxial side are more prominent than the others and are the continuations of the last formed pair of traces during the formation of the vascular connection to the leaf. There is profuse branching and anastomosing between the nearby vascular bundles towards the base of the stipe, but becomes rarer upwards. The vascular strands have, immediately outside the endodermis, a sheath of asymmetrically thickened cells, with their inner walls prominently thickened, blackish and with pit-connections. This ectendodermal sheath extends up to the basal swelling of the stipe and continues to the main lateral veins of the pinnae. The endodermal sheaths of the stipe bundles are continuous with that of the rhizome but the latter is little differentiated from the ground tissue.

Vascular supply to the pinna is established by the main lateral adaxial bundle and the lateral one next to it giving off a branch each (Text-Fig. 16, *p*). In some cases the basal pinnae of bigger leaves of *B. subcrenata* may receive three strands (two from the adaxial bundle of the stipe). In *B. subcrenata* the vascular strands fuse on entering the stalk of the pinna, so that the stalk and midrib has but a single bundle, which gives off lateral branches (main lateral veins of the lamina) alternately on either side. In *B. virens* on the contrary the two traces continue as separate bundles up the midrib (Text-Fig. 14), fusing only towards the apex of the pinna. Lateral branches are given off in alternate or subopposite succession, each bundle giving off branches to the side of the lamina nearest to it.

The stalk of the pinna is four-sided as is the rachis and possesses a prominent adaxial ridge with a groove on either side of it. Only the lower pinnae may be stalked in *B. subcrenata* and the stalk is up to 1·0 cm. in the bigger leaves. In *B. virens* all pinnae are stalked, the stalk being up to 2·0 cm. or more in the lower ones and up to 0·5 cm. in the upper. The pinnae in the former are ovate oblong, coriaceous, up to 25·0 cm. (excluding the attenuated apex) × 5·0 cm. in the lower pinnae and 10·0 cm. × 4·0 cm. in the upper, light-green, glossy, suddenly tapering at either end and with a prominent attenuated apex up to 5·0 cm. long. In *B. virens* they are oblong lanceolate, soft in texture, up to 20·0 × 2·0 to 2·5 cm. in the lower pinnæ and 15·0 × 2·0 cm. in the upper, deep-green, gradually tapering to either end, with an oblique upper base and with an acute or acuminate apex. The margin of the pinnae in *B. subcrenata* is slightly cartilaginous and is either smooth or wavy (with or without a few fine crenations), except towards the apex which is crenate or mostly serrate (Text-Fig. 17). In *B. virens* the margin is irregular towards the basal half, becoming crenate and finally sub-serrate towards the apex. Most of the pinnæ of the adult leaf in both spp. bear a vegetative, usually dormant, bud towards the apex situated on the midrib laterally on the upper surface (Text-Fig. 17, *b*.). The buds develop by the activity of a single apical meristematic cell differentiated early in the development of the pinna, and located lateral to the ridge over the midrib. Vascular connection to the bud is established by a branch of the midrib originating marginally from the midrib bundle, replacing a

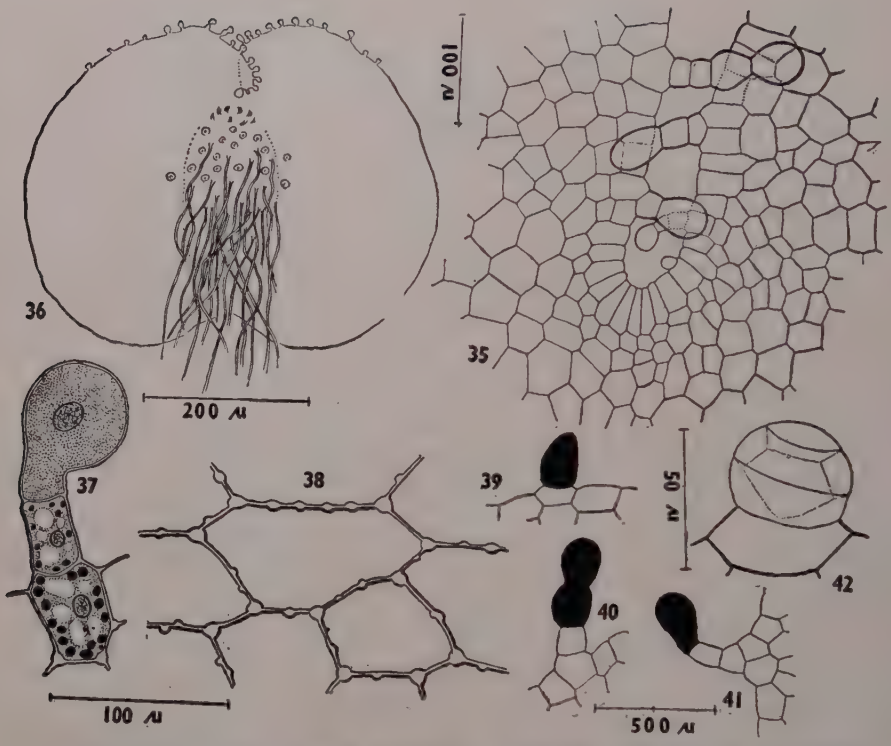


TEXT-FIGS. 17–34. Fig. 17. One basal sterile lateral pinna of *B. subcrenata* (*b.*, foliar bud). Fig. 18. Sporangium of *B. subcrenata*. Fig. 19. Base of a young sporangium of same showing attachment of stalk. Fig. 20. Apex of stalk of same. Fig. 21. Sporangium of *B. virens*. Fig. 22. Base of sporangium of same showing orientation of stalk. Fig. 23. Paraphyses. Fig. 24. Spore of *B. virens* in lateral view. Fig. 25. Same in polar view. Fig. 26. Structure of spore-wall. Figs. 27–34. Stages in development of prothallus showing germ filament, establishment of a meristematic apical cell and its replacement by an apical meristem.

main lateral vein to the lamina. This branch on entering the bud forms a solid stelar cylinder similar to the protostele of the rhizome of juvenile plants. In some cases the terminal pinna of the leaf resembles the lateral

ones, but mostly they are long and ribbon-shaped with the bud generally showing signs of development into daughter plants. The morphology and development of the bud to the adult condition are similar to those of rhizomes of juvenile plants. The terminal pinna in *B. subcrenata* may be up to 75·0 cm. or more long and 1·0 to 2·0 cm. wide, with a broadly wavy margin and with an oblique base. In *B. virens* they are up to 35·0 or 40·0 cm. long, generally 1·0 to 1·5 cm. wide and with the margin deeply wavy or in most cases pinnatisect, being cut up into obliquely ovate lobes the lamina between the lobes reduced to wings on either side of the midrib. In *B. virens* 2–3 pairs of prominent auricles occur below the terminal pinna, while in *B. subcrenata* they are absent or in some cases represented by one or two lobes. The number of pinnae per leaf is usually 5–6 subopposite pairs in the latter and 6–8 distinctly alternating pairs in the former.

The obvious difference between *B. subcrenata* and *B. virens* is the venation. In the former the main lateral veins from the midrib are 20–30 pairs (excluding the attenuated apex of the lamina), 0·3–0·5 cm. apart and distinct to very near the margin of the lamina (Text-Fig. 17). Each main lateral vein bears generally 8–12 alternate secondary veins each of which proceeds obliquely towards the margin and fuses with similar veins from the main lateral vein next in succession (Text-Fig. 44), thus forming a single row of hexagonal angular areolae between adjacent main lateral veins. From the point of fusion of the secondary veins one or two (very rarely more) tertiary veinlets proceed outwards and end blindly below the point of fusion of the next pair of secondary veins. The secondary veins towards the margin of the lamina are free, ending blindly at the margin. The costal row of areolae are prominent, pentagonal and devoid of free ending veinlets included inside. Rarely a few of the tertiary veinlets fuse between themselves forming minor areolae or fuse with the nearest pair of secondary veins, thus dividing the primary areolae. In *B. virens* the venation pattern is more complicated though the pinnae are smaller (Text-Fig. 43). The main lateral veins are 10–25 pairs per pinna (including apex) and are farther apart than in *B. subcrenata*, the distance between successive pairs being 0·5–1·0 cm. Each main lateral vein bears 3–6 pairs of secondary veins which branch and fuse in such a way that there are generally 3 rows of areolae between successive main lateral veins. Free-ending veinlets may or may not occur. On either side of the midrib there is a single row of prominent areolae, each areole extending from one main lateral vein to the other as in *B. subcrenata* but usually 6–7-sided. The main lateral veins lose their identity towards the margin, divide profusely and most of the branches fuse together forming one or two irregular rows of small areolae from the outer margin of which a few free-ending veinlets proceed towards the margin of the pinna. The venation of the ribbon-like terminal pinnae is simpler in both spp. The main lateral veins are far separated and only few secondary veins fuse to form areolae, the number of areolae being more in *B. virens*. In all pinnæ the venation is more prominent on the lower surface of the lamina. The midrib and main lateral veins show on the upper surface as fine ridges but



TEXT-FIGS. 35–42. Mature prothallus of *Bolbitis*. Fig. 35. Apex showing meristem and marginal hairs. Fig. 36. Entire prothallus in ventral view. Fig. 37. Optical section of a marginal hair. Fig. 38. Wing cells showing wall thickenings. Figs. 39–41. Types of marginal hairs. Fig. 42. Mature antheridium in lateral view.

protrude out of the general surface on the undersurface. The midrib of the elongated terminal pinna is more prominent than that of the others. Venation is more prominent in *B. subcrenata* than in *B. virens*.

Foliar appendages are small paleae basically similar to those on the stipe and rhizome but less clathrate and more irregular in outline. They are restricted to the lower surface, sparse, basally attached and may not have a cordate base. Mixed with them occur uniseriate 2- to 3-celled hairs resembling the marginal hairs of paleae. Appendages intermediate between the two also occur, and resemble those reported in spp. of *Elaphoglossum* (Bell, 1951). The epidermis is densely chlorophyllous in both spp. The upper epidermis is thick-walled composed of rather small cells with slightly wavy margin and regular in shape with the cells elongated parallel to the main lateral veins (Text-Figs. 47, 49). The lower epidermis is of much bigger cells with thin walls and deeply wavy outline, irregular in shape and elongated parallel to the main lateral veins. Stomata are profuse and each is almost en-

circled by the mother cell which is different from other epidermal cells in having a more even outline, regular shape and sometimes being broader than long (Text-Figs. 46, 48). In *B. subcrenata* and rarely in *B. virens* the cells subtending the mother cells also may be similar to them.

Fertile leaves are formed seasonally (November–March in the Western Ghats) and differ from the sterile ones in having a highly reduced lamina. The pinnae are *c.* 16·0×0·5–0·75 cm. (terminal one *ca.* 25·0 cm. in some cases) in *B. subcrenata* and *c.* 6·0–10·0×0·5 cm. or less (terminal one *c.* 15·0 cm.) in *B. virens*. The margin is incurved on the upper surface. In *B. subcrenata* the margin is often wavy while in *B. virens* it is usually subentire. The venation is also different (Text-Fig. 45), there being a midrib bearing alternating main lateral veins which divide and form two rows of areolae on either side of midrib. The costal areolae are narrow and long, extending from one main lateral vein to the next. A pair of the marginal areolae correspond with each of the costal ones. Sporangia occur all over the veins and the surface of lamina enclosed by areolae, but are absent on the midrib and near the margins where the veins do not reach. The incidence of sporangia is more on the veins and in young fronds sporangial formation initiates over the secondary veins at the points of their fusion. An abnormal fertile frond was observed in *B. subcrenata* collected from Kanchenkumri, in which the lamina, especially that of lower pinnae was only very slightly contracted (*c.* 2·5 cm. broad) but become progressively reduced in the upper ones, the uppermost pair being of normal form. The broad basal pinnae have the venation pattern of the sterile pinna. Towards the base of this pinna the sporangia are compital, being restricted to the points of fusion of secondary veins. Further up the pinna the sorus spreads over the secondary veins and the tertiary veins originating from the point of fusion of secondary veins. The tertiary veins regularly fuse with the secondaries above them so that towards the middle of the pinna the sori appear as broad bands between each pair of main lateral veins. The sporangia spread over the surface between the veins towards the apex of the pinna. The attenuated tip however has sori compital as in the basal region. In the upper pinnae of this leaf the condition gradually becomes normal with the venation modified, the transition being effected by gradual reduction in width of lamina resulting finally in the formation of only the costal row of areolæ and the fusion of the tertiary vein with the marginal vascular commissure between successive main lateral veins.

Mature sporangia are black and shining. Paraphyses occur, but are too small and inconspicuous, so as to be easily overlooked among the much elongated stalks of sporangia. They are club-shaped (Text-Fig. 23), uniseriate, multicellular (2–5 celled) hairs, resembling some of the foliar appendages and are deep brown in colour. The sporangium in *B. subcrenata* (Text-Fig. 18) has a long stalk 7–10 cells long and 2 cells thick except towards the apex where it is 3-celled (Text-Figs. 19, 20). The stalk of young sporangia consists of only 2 rows of cells one in

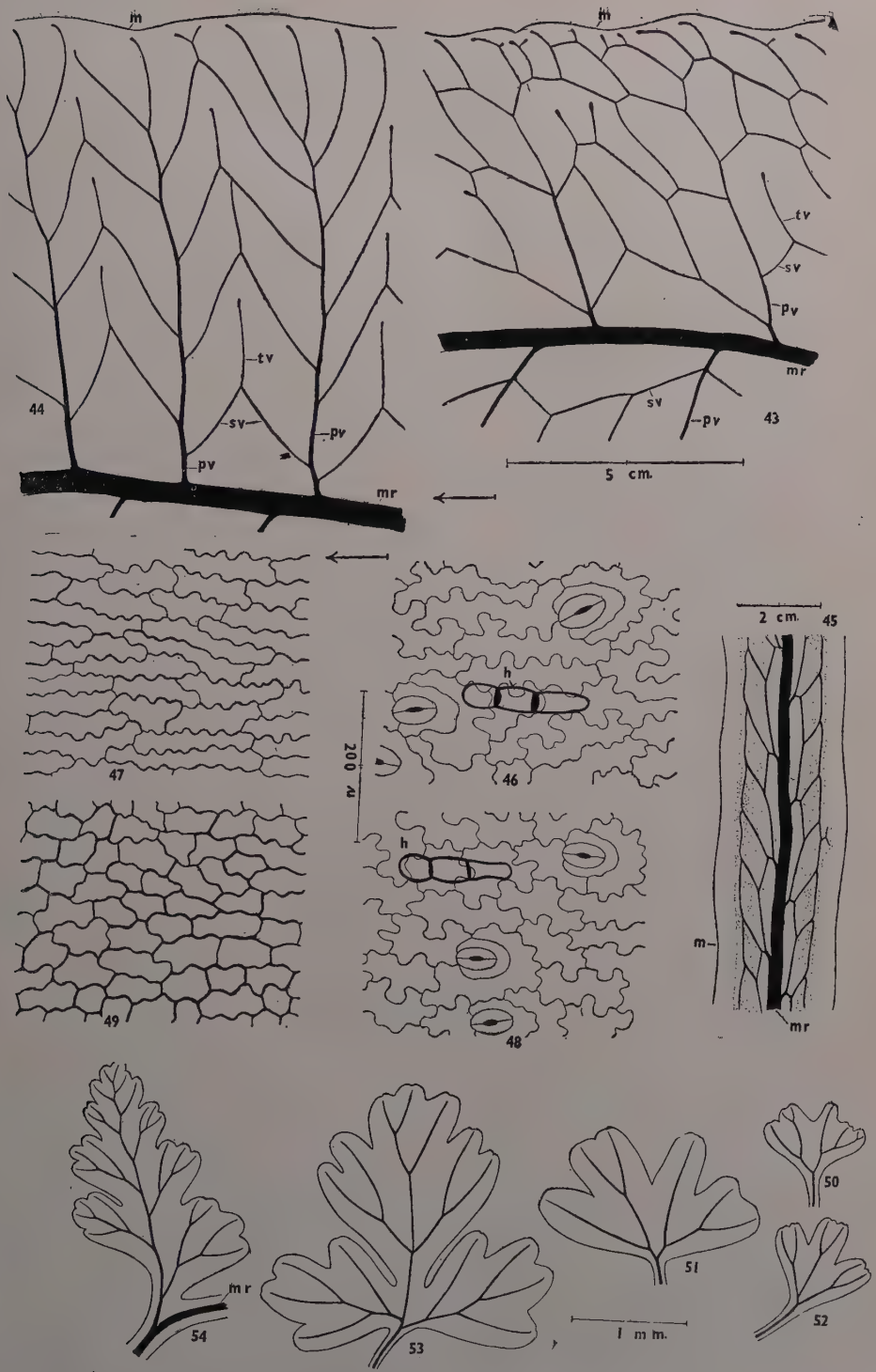
front of the other. Cells of the annulus and stomium constitute a circle round the sporangial head the annulus abutting laterally on the top of the uppermost stalk cell and the basal cell of the stomium abutting on the other stalk cell laterally, so much so that at this stage the annulus and stomium are lateral to the stalk. Later the basal wall cell of the sporangial head which abuts on the ends of the annulus and the stomium protrudes as a papilla over and partly covering them. This papilla later becomes usually 2–4 cells long and forms the 3rd row of the stalk. The annulus is usually 19–24 (range: 14–26) cells long and abuts on the stomium which is 7–9 cells long, with four prominent lip cells. Each sporagnium is borne on a small conical protuberance of the lamina surface. Sporangia of *B. virens* differ in having an annulus of usually 13 (range: 12–15) cells (Text-Figs. 21, 22).

The spores (Text-Figs. 24, 25) are bilateral, planoconvex in lateral view, with a short laesura, medium-sized ($P \times E_1 \times E_2$ being on an average $33 \times 40 \times 32\,\mu$ in *B. subcrenata* and $24 \times 38 \times 26\,\mu$ in *B. virens**), with a highly wrinkled loose perisporium usually protruding up to $8\,\mu$ but sometimes up to $16\,\mu$ from the exine surface. Sexine is slightly thicker than nexine (Text-Fig. 26), not clearly differentiated and is smooth in both the spp.

In cultures the spores germinated in late November. The exine ruptures at the laesura and the first rhizoid protrudes out, soon followed by a germ filament originating lateral to the rhizoid. Within a fortnight the germ filament becomes 5–8 cells long with cells broader than long and densely chlorophyllous (Text-Fig. 27). Flattening of the filament sets in soon by longitudinal divisions of cells in the anterior part of the filament including the terminal cell (Text-Fig. 28). An obconical apical cell is established in the usual way (Text-Fig. 29), by the formation of an oblique wall in one of the daughter cells of the terminal cell after longitudinal division. A spatulate prothallus is soon formed by the activity of this apical cell (Text-Figs. 30, 31). Antheridia may be formed superficially (rarely marginally) by spatulate prothalli. Many of the marginal cells towards the basal end of the prothallus produce rhizoids. The apical cell is soon replaced by an apical meristem formed in the usual way (Text-Fig. 32). In rare cases an apical cell may not at all be formed, an apical meristem being directly established by spatulate prothalli. Prothalli nearly two months old begin to form the characteristic apical notch with the meristem lodged at its bottom (Text-Figs. 33, 34). Superficial rhizoids and antheridia are formed at this stage of development. Archegonia are produced by cordate prothalli nearly 3 months old. Some of the vigorously growing prothalli may be entirely female, producing only archegonia, while the others have antheridia and archegonia together though the former are formed earlier in development.

The mature prothallus (Text-Fig. 36 and Plate I, Fig. VIII) is cordate, broader than long (*c.* 1·0 cm. across), with a prominent apical notch

* Measurements are based on acetolyced spores mounted in glycerine jelly.



TEXT-FIGS. 43–54.

TEXT-FIGS. 43–54. Leaf morphology. Fig. 43. Venation pattern in *B. virens* (the arrow points to the apex of the pinna). Fig. 44. Same in *B. subcrenata*. Fig. 45. Venation pattern in a fertile pinna of *B. subcrenata* (shaded areas sporangiferous). Fig. 46. Lower epidermis of *B. subcrenata* (the arrow points to the margin of lamina). Fig. 47. Upper epidermis of same. Fig. 48. Lower epidermis of *B. virens*. Fig. 49. Upper epidermis of same. Figs. 50–53. Entire juvenile leaves showing succession of venation patterns. Fig. 54. One pinna of a juvenile leaf representing stage next to the one in Fig. 53. (*h.*, foliar hair, *m.*, margin of pinna; *pv.*, main lateral vein; *sv.*, secondary vein; *tv.*, tertiary vein.)

having the lateral lobes on either side of the notch overlapping considerably, and a prominent broad midrib bearing sex organs and rhizoids ventrally. The wing cells have prominent collenchymatous thickenings localized on the side-walls and at the corners (Text-Fig. 38). The thickenings appear as bright hyaline circular areas under the microscope (Plate VIII, Fig. 3), giving a characteristic appearance to the thallus. Thickenings appear only in cordate thalli. Multicellular marginal hairs occur towards the anterior end of mature thalli (Text-Figs. 35, 36), the posterior half being naked. The frequency of hairs vary with individual thalli, some having very few hairs sparsely distributed while others have them in profusion, most of the marginal cells towards the meristem bearing hairs. Young gametophytes are entirely naked, the hairs being produced only by mature thalli after the formation of the midrib, with the result that hairs are absent on the posterior half of mature thalli. The hairs (Text-Figs. 39–41 and Plate VIII, Fig. 2) are uniseriate and multicellular. Each hair (Text-Fig. 37) has a stalk 1–4 cells long bearing a swollen terminal cell. The stalk cells are thin-walled, with a few included chloroplasts, highly vacuolated protoplasm and a nucleus smaller in size compared to that of other prothallial cells. The terminal cell is deep-brown to black in colour, probably tannin containing, with uniformly dense contents, thin-walled and with a bulbous apex and a prominent nucleus. In some cases the terminal cell and the penultimate cell become swollen (Text-Fig. 40) and acquire dense contents. Each hair originates as a papillose protuberance on a marginal cell, 2–3 cells away from the meristem, and is cut off by a basal wall. The papilla elongates and becomes 2–5-celled by transverse divisions (Text-Fig. 35). The subtending prothallial cell generally divides longitudinally and in many cases protrudes out of the general surface (Text-Fig. 41). The nucleus of the terminal cell of the hair enlarges to double its size and the cell contents become dense and highly granular (Text-Fig. 37). The hair elongates and the stalk cells become vacuolated, while the terminal cell becomes globose, there being no vacuolation of the contents. As the hair matures, the contents of the terminal cell become deep-brown. The mature hairs have sparsely distributed chloroplasts.

Sex organs are of the type usual in leptosporangiates. The antheridia are globular (Text-Fig. 42), slightly flattened dorsiventrally and have the usual type of development. The opercular cell is single and is thrown off to release the sperms.

Gametophytes 3 months old produce sporelings. Sporelings are formed in profusion under cultural conditions, only a single sporeling

being observed per thallus. Generally the first cotyledonary leaf (Text-Figs. 50, 51) is broadly wedge-shaped with the base forming an angle of nearly 150° and is supplied by a single vascular bundle which forks two to three times. The margin is lobed, each segment having one veinlet towards its middle. Weak sporelings may have leaves with simpler lamina, while some of the vigorous prothalli produce sporelings with the first leaf itself representing the next stage in development, where the apex of the lamina is emphasised, the middle lobe being longer than the others (Text-Fig. 52). A midrib is differentiated, originating from the base of the lamina just above the first dichotomy of the vascular strand so that the veins to the side lobes of the lamina appear as branches of the central midrib. The transition from the midribless to the midribbed stage is rather sudden, the latter stage being represented usually by the second leaf and in a number of cases by the first leaf itself. Generally in the third leaf the vascular supply of the lowest pair of lobes becomes pinnate in pattern (Text-Fig. 53) with a midrib bearing lateral branches alternately. In succeeding leaves the lamina becomes divided pinnately, each lobe receiving one main lateral vein from the midrib (Text-Fig. 54). The adult form is attained by plants over an year old.

The first cotyledonary leaf is generally devoid of trichomes. Unicellular papillate hairs occur profusely on margins and scattered on both surfaces of leaves in which a midrib is established. The hairs are formed superficially on the outer wall of the epidermal cells and are usually cylindrical with highly vacuolated hyaline cytoplasm and a few chloroplasts. Each hair has a prominent light yellow extracellular secretion forming a cap towards the tip. The apical caps dissolve easily in acetic acid and so are soon lost in ordinary preservatives. Hairs with transverse septæ occur especially on later formed leaves. The adult type of hairs are formed only on later formed leaves and is initiated towards the base of stipes, gradually spreading upwards on successive leaves.

Discussion

Holttum (1947) regards *Bolbitis* as a Dennstaedtioid fern and includes it along with *Egenolfia*, *Elaphoglossum*, *Teratophyllum*, etc., in his *Lomariopsideae*. He considers the family to have originated probably on a line near *Davallia*. Christensen (1938) regards *Bolbitis* as of Dryopteroid origin, but considers *Elaphoglossum* as a separate subfamily Elaphoglossoideae " of doubtful systematic position and perhaps polyphyletic ". According to Ching (1940) *Bolbitis* is an Aspidioid fern distinct from *Egenolfia* (which is Dryopteroid) and *Elaphoglossum* (Elaphoglossaceae). Copeland (1947) includes *Bolbitis* along with *Egenolfia et al.* in his Aspidiaceae but does not suggest any relationship with *Elaphoglossum*.

The present studies tend to support the view of Holttum that *Bolbitis* is near to *Elaphoglossum* phylogenetically. Through the detailed studies of Bell (1950–56) and Stoky & Atkinson (1957) the morpho-

logy of the sporophyte and gametophyte of *Elaphoglossum* is comparatively better known than that of the majority of ferns. Unfortunately we know little about the morphology of the other genera with which relationship is suggested.

The paleae in the spp. of *Bolbitis* studied conform with the paleae of *Elaphoglossum* especially of *E. tectum*, *E. chartaceum*, etc., in which they are " deeply cordate and auriculate at the base and the auricles are widely and closely overlapping, so that the attachment appears, at first sight, set in from the margin " (Bell, 1951). The foliar appendages of *Bolbitis* are not as complicated as in many spp. of *Elaphoglossum*, but are, however, comparable in being brownish, thick-walled and terminated by a gland. The dorsiventrally flattened rhizome with leaves restricted to the upper surface and each leaf associated with an abaxially placed dormant bud is met with in many spp. of *Elaphoglossum*. A swollen parenchymatous area occurs towards the base of the stipe of *E. latifolium*, etc., and though occurring towards the very base of the stipe the parenchymatous swelling in *B. subcrenata* is comparable. The ærenchymatous ridge on either side of the stipe finds its parallel in *Elaphoglossum*. The flanges towards the base of the stipe in *B. subcrenata* are comparable to similar structures in *E. latifolium*.

The vascular structure of the rhizome of *Elaphoglossum* is highly complicated in many spp. due to presence of more than two rows of leaves and extreme shortness of rhizome. But the basic pattern as exemplified by *E. latifolium* (Bell, 1950) is essentially the same as in *Bolbitis*, both having a broad ventral meristele and a small median dorsal one joined at regular intervals with either margin of the ventral meristele alternately, to form the leaf gaps. But in *E. latifolium*, etc., the bud trace originates independently of the leaf traces though originating simultaneously and occasional cases of vascular connection between the bud and leaf traces " suggesting a tendency for the bud trace to be connected with the leaf trace " are reported (Bell, 1951). A developing lateral bud in *E. hirtum* is described by Bell (1951) as having a protostele at the very base which becomes grooved on the dorsal surface and produces traces from both sides of the groove to supply each leaf. If the pattern followed by the branch is to be taken as an indication of the pattern in the main rhizome of *Elaphoglossum*, the condition in *Bolbitis* is also the same. If ontogeny reveals any indication of phylogeny it may be that the complicated stelar pattern of *Bolbitis* and *Elaphoglossum* is evolved from an ancestor with a gutter-shaped vascular cylinder. In this connection it may be noted that an almost similar stelar pattern is reported in *Leucostegia pallida* (Kachroo, 1956). The leaf-associated branches in this sp. originate from the abaxial end of the leaf gap and are not united to the leaf traces (which are only two per leaf) originating further up the gap. *L. immersa* (Kachroo, 1955) has a stele of similar pattern, but with accessory vascular commissures between the dorsal and ventral meristeles. The ect-endodermal sheath of the petiolar vascular bundles of *Bolbitis* finds its parallel in *Elaphoglossum*. The epidermal cells of the lamina are chlorophyllous in both the genera and the relationship between the

stomata and mother cells is comparable (in *E. latifolium*, *E. villosum*, etc.). Size and morphology of the spores of *B. subcrenata* and *B. virens* compare favourably with the spores of *E. gayanum*, *E. tectum*, etc. (Stokey and Atkinson, 1957), though some spp. of *Elaphoglossum* like *E. papillosum* and *E. boragineum* are reported to have a different type of spore.

The gametophytes of *Bolbitis*, however, show distinctive features which are not comparable to those of *Elaphoglossum* or *Rhipidopteris*, the two genera of which gametophytes are known. Even recognising the tendency of *Elaphoglossum* to develop long-lived gametophytes with ribbon-like form as an adaptation to the epiphytic habit, does not solve the problem. The nature of development of the thallus, its general morphology including the characteristic thickening of the wall cells and the trichomes are different from those of *Elaphoglossum*. The hairs of *Bolbitis* do not compare with the types of prothallial hairs reported so far, though a comparison may be made to the hairs reported in some of the *Davalliaceae* like *Leucostegia* (Kachroo, 1955) in which multicellular, uniseriate hairs with a terminal glandular cell comparable to the hairs of *Bolbitis* occur. However, these hairs resemble the foliar hairs of the sporophyte in morphology pigmentation and development, thus lending support to the suggestion made by the author in an earlier communication (Nayar, 1956) that in many spp. of ferns there may possibly be some correlation between the gametophytic and sporophytic trichomes. The peculiar type of thickenings on the wall of the prothallial cells are of the type characteristic of the Schizæaceæ especially *Anemia* (Stokey, 1951) and is not so common in other ferns. The phylogenetic value of this feature seems, in the present state of our knowledge of fern prothalli, to be dubious.

To sum up, it seems that *Bolbitis* is nearer to *Elaphoglossum* as suggested by Holttum rather than distinct from it as suggested by other pteridologists. Though the sporophyte morphology reveals much in common between the two genera the gametophytes are so distinctive that the suggestion of a close relationship is not warranted. *Bolbitis* appears to be more primitive than *Elaphoglossum*. A clear understanding of the problem can, however, only be had after studying the morphology of the other genera of Holttum's Lomariopsidoideae, especially *Egenolfia*, *Teratophyllum* and *Lomagramma*.

Summary

Detailed morphology of the sporophytes and gametophytes of *Bolbitis subcrenata* and *B. virens* is studied. The rhizome is creeping, dorsiventral, having two alternating rows of closely set leaves with associated abaxial buds on the dorsal surface, irregular leaf-opposed transverse rows of roots on the ventral surface and covered by clathrate pseudopeltate paleae with overlapping basal auricles and bearing terminal and marginal uniseriate glandular hairs. The vascular cylinder of the rhizome is a solenostele with two rows of large, overlapping leaf gaps on the dorsal surface, which virtually split the stelar cylinder into a

broad, root bearing, ventral meristele and a small dorsal one mainly concerned with the bearing of leaf traces. Leaf traces are 5–10 per leaf and the bud trace originates as a branch of the abaxial trace to the leaf. The branch trace soon after origin gives off a root trace.

Leaves are heterophyllous, pinnate with articulated pinnæ and with the apical pinna of sterile leaves usually ribbon-shaped and non-articulat d. Sterile pinnae mostly bear a dormant bud lateral to the midrib towards the apex on the upper surface. The venation pattern is described. Paleae occur on the stipe and sparsely over the lamina, those on the latter being much smaller and reduced to hairs in some cases. Pinnae of fertile leaves are much reduced and linear with acrostichoid distribution of sporangia mingled with paraphyses. The stipe has a swollen base and show prominent aerenchyma ridges continuous with the lamina on either side. Pinna trace originates as a multiple strand from the adaxial bundle and the lateral bundle next to it, of the rachis. There is an ectendodermal sheath of asymmetrically thickened cells in the foliar bundles.

Spores are bilateral and perisporiate. The development and morphology of the prothallus is described. Mature prothallus is cordate with a prominent midrib and bears characteristic marginal trichomes.

The morphological features of the sporophyte and gametophyte are compared with those of *Elaphoglossum* and it is shown that the association of *Bolbitis* with *Elaphoglossum* as done by Holttum is probaby more justifiable than the attitude adopted by most other pteridologists.

Acknowledgements

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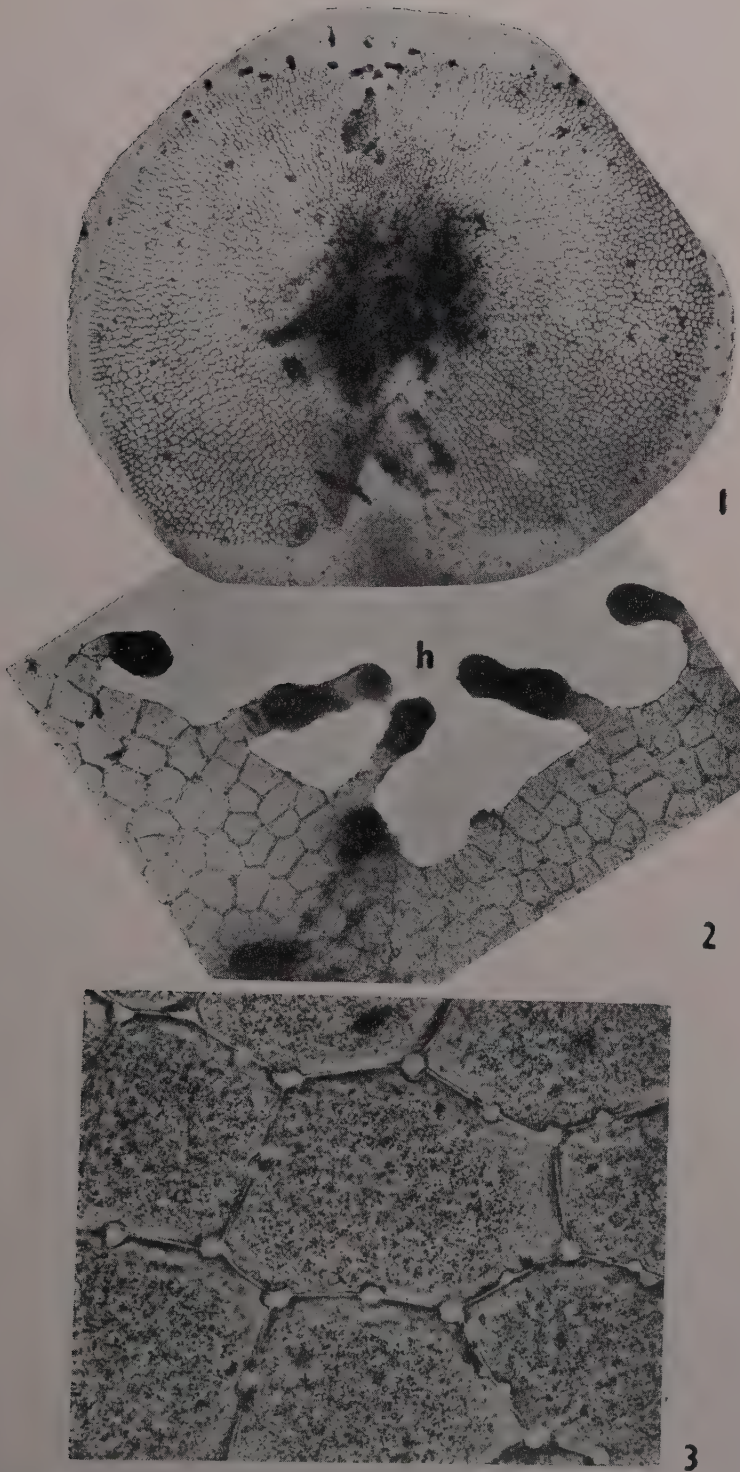

B. K. Nayar

FIGS. 1–3

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EXPLANATION OF PLATE VIII

FIGS. 1–3. Morphology of the mature gametophyte of *B. subcrenata.* Fig. 1. Entire prothallus. Fig. 2. Apex of same showing marginal hairs (*h*). Fig. 3. Wing cells.

ACCESSORY CHROMOSOMES IN *SORGHUM NITIDUM* PERS.

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Sorghum nitidum Pers., of the sub-genus *Para-Sorghum*, occurs naturally in two chromosomal races, *viz.*, $2n = 10$ and 20 (Krishnaswamy *et al.*, 1956). While determining the chromosome numbers of some recent additions to the type collection of this species, a clump revealed six bivalents during meiosis and the two extra chromosomes were observed to be accessory chromosomes. The preliminary studies on the cytology of this plant are presented in this paper.

Material and Methods

The plant under study was collected in a hill near Coimbatore at an altitude of 4,000′.

For the study of meiosis, panicles were fixed in propionic alcohol (1 : 3) and the anthers squashed in propiono carmine. Root-tips were fixed in Lewitsky's fluid, sectioned by the paraffin method at 12 microns thickness and stained in crystal violet. The somatic chromosomes were also studied by Feulgen-acetocarmine squashes of the root-tips after pretreatment with paradichlorobenzene for three hours and hydrolysis in N.HCl for 25 minutes.

Observations

The clump with the $n = 6$ chromosome number did not reveal any difference in external morphology from the normal ones.

At diakinesis, six bivalents, one of which is nucleolar, are formed regularly (Pl. IX, Fig. 3). Univalents and associations higher than bivalents were never met with. Compared to diakinesis in normal plant (Pl. IX, Fig. 1), it may be noted that the B-bivalent forms clear chiasmata and there appears to be no appreciable difference in size between the B and any of the other bivalents.

At I metaphase, there is a normal equatorial plate with six bivalents (Pl. IX, Fig. 4). Rarely the chromosomes of the B-bivalent were observed to separate precociously at this stage. The distribution at I anaphase is usually equal and regular (Pl. IX, Fig. 5) except for an

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occasional disjunction bridge (Pl. IX, Fig. 6). The I telophase was usually clean (Pl. IX, Fig. 6) but a laggard was observed in a solitary case (Pl. IX, Fig. 5). The second division was normal (Pl. IX, Figs. 7 and 9), but here also chromatin bridges were rarely met with (Pl. IX, Fig. 8).

The size and fertility of the pollen grains were studied in both the + 2 B plant (Pl. IX, Fig. 10) and the normal ones and are tabulated below:

	+ 2 B plant	Normal plant
Pollen fertility (%)	60	78
Average pollen size (in microns) ..	64·9	57·7
Maximum pollen size (in microns) ..	79·5	68·9
Minimum pollen size (in microns) ..	47·7	47·7

Several root-tips were analysed by the paraffin method and also by the rapid squash technique to determine the somatic chromosome number and the variation, if any, but in all cases the number was observed to be only $2n = 10$ without any exception.

Heteropycnosis or differential staining of the chromosomes was not observed in any of the meiotic stages including pachytene (Pl. IX, Fig. 2), but no special techniques were followed to study the same.

Discussion

Accessory or B-chromosomes have been previously recorded in another *Para-Sorghum*, *S. purpureosericeum* in which 0–6 of them were observed during meiosis (Janaki Ammal, 1940). Darlington and Thomas (1941) investigated the same material and reported three kinds of these B-chromosomes, *viz.*, large standard chromosome (M), large iso-chromosome (L) and short chromosome (S). Again, Garber (1950) observed that two of these (M and S) were present in the subspecies *deccanense* and *typicum* of *S. purpureosericeum*. He also quoted O'Mara's record of B-chromosomes in the subspecies *dimidiatum*. Since the two B chromosomes in *S. nitidum* regularly pair with each other and since they are equal in size with the other bivalents, they may be classified under the standard (M) type.

The elimination of the B-chromosomes from the root tissue, as in *S. nitidum*, has previously been recorded only in *S. purpureosericeum* (Janaki Ammal, 1940), two strains of *Poa alpina* (Müntzing, 1954; Müntzing and Nygren, 1955) and lastly in *Panicum coloratum* (Swaminathan and Joginder Nath, 1956).

Type collections of *S. nitidum* are being intensified to make a fuller study of the frequency of the accessory chromosomes.

Summary

The meiosis in a clump of *S. nitidum* with $2n = 10 + 2$ B chromosomes has been studied. The two accessory chromosomes are of the standard type and pair regularly with each other. These chromosomes are eliminated from the root tissue just as in the other *Para-Sorghum*, *S. purpureosericeum*.

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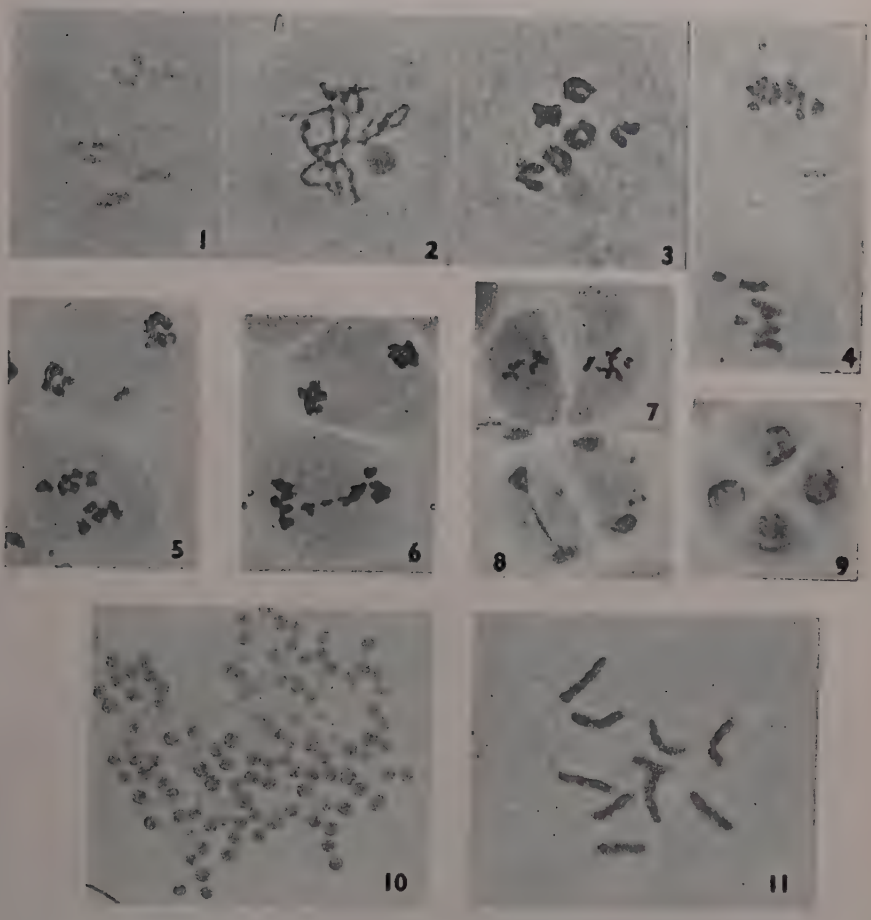
Explanation of Plate IX

Fig. 1. Diakinesis in normal plant ($n = 5$), ×789.

Figs. 2–10. Meiosis in the plant with 2 B-chromosomes ($2n = 10 + 2$ B). Fig. 2. Pachytene, ×789. Fig. 3. Diakinesis with six bivalents, ×789. Fig. 4. I metaphase—the upper cell with six bivalents and the lower one with the B-bivalent desynapsed precociously, ×710. Fig. 5. I Anaphase showing 6/6 distribution and I telophase with a laggard, ×710. Fig. 6. I Anaphase with disjunction bridge and normal I telophase, ×710. Fig. 7. II Metaphase; $n = 6$ in each cell, ×552. Fig. 8. II Telophase with disjunction bridge, ×552. Fig. 9. Tetrad, ×552. Fig. 10. Pollen grains, ×67.

Fig. 11. Somatic chromosomes ($2n = 10$) showing the elimination of the B-chromosomes in the root cells, ×1,499.



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FIGS. 1–11

GENETIC STUDIES IN BARLEY

II. Inheritance of Fertility of the Lateral Florets and Certain Other Characters

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TWO-ROWED *vs* six-rowed condition which is dependent upon the fertility of the lateral florets is one of the important morphological characters that has attracted the attention of workers interested in the breeding of the barley crop. Harlan (1918) classified cultivated varieties of barley into four species on the basis of the lateral florets, *viz.*, (i) six-rowed barley, with all rows similar in fertility and showing development of hoods or awns (*H. vulgare*), (ii) intermediate barley with partial fertility of the lateral florets which never bear hoods or awns (*H. intermedium*), (iii) two-rowed barley, in which the lateral florets are staminate and produce no grains (*H. distichon*) and (iv) two-rowed barley, with rudimentary lateral florets, devoid of sex organs (*H. deficiens*). More or less similar classifications have been made by others also. Extensive studies were conducted by various workers to find out the genetic possibilities of these forms but the results obtained by them are not in agreement so far as the factorial interpretations are concerned. A number of workers who studied the inheritance of two and six rows character in barley obtained results which indicated that the parental forms differed by a single pair of factors, while others observed that some crosses gave intermediums and explained the results on the hypothesis that the parental forms differed in two or more factor pairs (see Smith, 1951).

The genetics of hoods and awns has also been a subject of considerable interest, one reason being that as a group awnless and hooded varieties do not usually have the yielding capacity of the awned types. Morphologically awn or lemma projection, which is an extension of the vascular system of the lemma into a pointed appendage, varies in different varieties from several centimetres in length to complete absence. These variations give rise to various awn types, long-awned, short-awned, awnletted and awnless. Another variation in the lemma projection is the hooded condition in which the normal awn is replaced by a trifurcate structure. The hood, though commonly sessile, may be elevated to varying degrees in certain varieties. A detailed review on the inheritance of awns and hoods is given by Smith (1951).

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The present paper mainly deals with the studies undertaken to collect data on the mode of inheritance of the fertility of the lateral florets in crosses of *H. vulgare* with *H. distichon* and *H. vulgare* with *H. deficiens* forms and the inheritance of awns and hoods in crosses involving long-awned and hooded (sessile) varieties. The inheritance of some other characters like length of the outer glume awns, leaf shape, early growth habit and heading date was also studied in these crosses. Part of this material was also used for studies on the mode of inheritance of pigmentation in various plant parts and these results have been reported by us in an earlier paper (Murty and Jain, 1959).

Material and Methods

Eight crosses, *viz.*, E.B.* 171×E.B. 417, E.B. 177×E.B. 417, K. 251×E.B. 438, K. 251×E.B. 132, C. 138–2×E.B. 132, K. 251 × E.B. 145, N.P. 13×E.B. 145 and C. 138 – 2×E.B. 145 were studied with reference to the mode of inheritance of the following characters.

Character	Crosses
(1) Fertility of the lateral florets	
(*a*) *H. vulgare*×*H. distichon*	(i) K. 251×E.B. 438
	(ii) E.B. 171×E.B. 417
	(iii) E.B. 177×E.B. 417
(*b*) *H. vulgare* ×*H. deficiens*	(iv) K. 251×E.B. 132
	(v) E.B. 138 – 2×E.B. 132
(2) Hoods *vs* long awns	(i) K. 251×E.B. 132
	(ii) C. 138 – 2×E.B. 132
(3) Long *vs* short outer glume awns	(i) K. 251×E.B. 438
	(ii) E.B. 171×E.B. 417
	(iii) E.B. 177×E.B. 417
	(iv) K. 251×E.B. 132
	(v) C. 138 – 2×E.B. 132
(4) Broad *vs* narrow leaves	(i) K. 251×E.B. 438
(5) Early habit of growth	(i) K. 251 ×E.B. 438
(6) Heading date	(i) K. 251×E.B. 438
	(ii) K. 251×E.B. 145
	(iii) N.P. 13×E.B. 145
	(iv) C. 138 – 2×E.B. 145

* Accession numbers given to exotic barley types in the collection at the Indian Agricultural Research Institute, New Delhi.

The study was made through F_1, F_2 and F_3 generations in all the crosses except K. 251×E.B. 145, C. 138–2×E.B. 145 and N.P. 13× E.B. 145 which were studied only in F_1 and F_2 generations for heading date. One of these three crosses was studied at two locations, *viz.*, Delhi and Wellington (Nilgiris) and the other two only at Wellington. In addition, the back cross generation was studied in some crosses. The parental varieties showed differences in the following characters.

Variety	Type of spike	Glume extension	Type of outer glume awns	Leaf shape	Early growth habit	Heading date
E.B. 132 ..	*Deficiens*	Hooded (sessile)	Short	Broad	Erect	Early
E.B. 145 ..	*Distichon*	Awned (long)	,,	Medium	Semi-spreading	Mid-late
E.B. 171 ..	Six-rowed	,,	Long	Broad	Erect	Early
E.B. 177 ..	,,	,,	,,	,,	,,	,,
E.B. 417 ..	*Distichon*	,,	Short	Narrow	Semi-spreading	Medium
E.B. 438 ..	,,	,,	,,	,,	,,	Mid-late
K. 251 ..	Six-rowed	,,	Long	Broad	Erect	Early
C. 138–2 ..	,,	,,	,,	,,	,,	,,
N.P. 13 ..	,,	,,	,,	,,	,,	,,

Experimental Results

1. *Inheritance of fertility of the lateral florets*

(*a*) H. vulgare×H. distichon *crosses*.—The mode of inheritance of the two-rowed (*distichon*)×six-rowed type of spike was studied in three crosses, *viz.*, K. 251×E.B. 438, E.B. 171×E.B. 417 and E.B. 177× E.B. 417 in the F_1, F_2 and F_3 generations. In addition, the back cross generation was also studied in E.B. 171×E.B. 417. The F_1's and F_2's of these crosses were studied for two years. During the year, 1956–57, the segregating population was classified into two groups, *viz.*, non-six-rowed and six-rowed. In the year, 1957–58, however, detailed observations on the development of the lateral florets were recorded. The segregation ratios obtained in these crosses in the F_2 and B_1 generations along with the parental types and F_1 generations are given in Tables I (*a*) and (*b*) respectively for the two years.

TABLE I (*a*)

Inheritance of non-six-rowed vs *six-rowed in* H. vulgare × H. distichon *crosses in the* F_2 *generation* (1956–57)

Material	Number of plants			X^2	P. value
	Non-six-rowed	Six-rowed	Total		
Cross: K. 251 × E.B. 438:					
K. 251	..	30	30		
F_1	12	..	12		
F_2 observed	113	40	153		
F_2 expected (3 : 1)	114·75	38·25	..	0·106	·80–·70
E.B. 438	35	..	35		
Cross: E.B. 171 × E.B. 417:					
E.B. 171	..	24	24		
F_1	6	..	6		
F_2 observed	140	49	189		
F_2 expected (3 : 1)	141·75	47·25	..	0·086	·80–·70
E.B. 417	36	..	36		
Cross: E.B. 177 × E.B. 417:					
E.B. 177	..	36	36		
F_1	7	..	7		
F_2 observed	73	35	108		
F_2 expected (3 : 1)	81	27	..	3·16	·10–·05
E.B. 417	36	..	36		

Note.—Many of the plants were damaged by a hailstorm in March 1957, and this is the reason why the number of the F_2 plants shown in this table is rather low.

It will be seen from data presented in Table I (*a*) that the F_1 in all the crosses was non-six-rowed and the X^2 value showed a good fit to a ratio of 3 non-six-rowed : 1 six-rowed in the F_2. Detailed observations on the fertility of the lateral florets taken in 1957–58 are presented in Table I (*b*). In the F_1 of the cross K. 251 × E.B. 438, the lateral florets were slightly more developed than the *distichon* form E.B. 438. These lateral spikelets were slightly tipped and partially fertile (2–3 grains per year) (Pl. X, Fig. 1). In the F_2, 3 phenotypic classes, *viz.*, two-rowed, infertile intermediates like F_1 and six-rowed in the ratio of 1 : 2 : 1 were observed. This character was obviously controlled by one factor pair in the cross. In the crosses E.B. 171 × E.B. 417 and E.B. 177 × E.B. 417 the lateral florets were well developed, highly fertile

TABLE I (*b*)

Inheritance of fertility of the lateral florets in the crosses H. vulgare×H. distichon *in the* F_1, F_2 and B_1 *generations* (1957–58)

Material	Number of plants				X^2	P. value
	Two-rowed	Intermediate	Six-rowed	Total		
Cross: K. 251×E.B. 438:						
F_1	.. ..	12	..	12		
F_2 observed	.. 103	178	83	364		
F_2 expected (1:2:1)	.. 91	182	91	..	2·373	·50–·30
Cross: E.B. 171×E.B. 417:						
F_1	.. ..	11	..	11		
F_2 observed	.. 105	296	130	531		
F_2 expected (3:9:4))	.. 99·57	298·68	132·75	..	0·395	·90–·80
F_1×E.B. 171 observed	.. ..	7	12	19		
F_1×E.B. 171 expected (1:1)	..	9·5	9·5	..	1·315	·30–·20
Cross: E.B. 177×E.B. 417						
F_1	.. ..	7	..	7		
F_2 observed	.. 94	274	124	492		
F_2 expected (3:9:4)	.. 92·25	276·75	123·0	..	0·069	·98–·95

(90–95%) and the awn length varied from 2–4 cm. (Pl. X, Fig. 1). In the F_2 generation, intermediates, intermediums, two-rowed and six-rowed types were observed. However, for the sake of genetical interpretation, intermediums and intermediates were combined. The data in Table I (*b*) show that the F_2 segregation gave a good fit to a ratio of 9 intermediates and intermediums: 3 two-rowed: 4 six-rowed, showing that two factor pairs were operating in determining the inheritance of lateral florets in these crosses. The back cross data in E.B. 171× E.B. 417 showed a good fit to a ratio of I intermediates: 1 six-rowed types.

The F_3 families of the three crosses were also studied and the data are given in Table I (*c*).

TABLE I (*c*)

Segregation in F_2 determined by F_2 breeding behaviour, for fertility of the lateral florets

F_2 Genotypes	*vvii* *vvI^{h}i* *vvI^{h}I^h*	*Vvii*	*VvI^{h}I^h*	*VvI^{h}i*	*VVii*	*VVI^{h}i*	*VVI^{h}I^h*	Total	X^2	P. Value
F_3 segregating classes	Six-rowed, breeds true	Segregates into two-rowed, infertile intermediates and six-rowed	Segregates into fertile intermedium, fertile intermediates and six-rowed	Segregates for all classes as F_1	Two-rowed, breeds true	Segregates into two-rowed and infertile intermediums	Partly fertile intermedium, breeds true			
Ratios	4	2	2	4	1	2	1			
				Cross: *K. 251 × E.B. 438 (vvii × VVii)*						
F_3 observed	22	42	..	..	16	..	..	80		
expected (1 : 2 : 1)	20	40	..	..	20	..	..		1·1	·70–·50
				Cross: *E.B. 171 × E B. 417 (vvI^{h}I^h × VVii)*						
F_3 observed	32	16	7	23	13	3	4	98		
expected	24·5	12·25	12·25	24·5	6·12	12·25	6·12		19·63	∠·01
				Cross: *E.B. 177 × E.B. 417 (vvI^{h}I^h × VVii)*						
F_3 observed	30	9	10	21	13	12	3	98		
expected	24·5	12·25	12·25	24·5	6·12	12·25	6·12		12·31	·10–·05

Eighty families were studied in the F_3 generation in the cross K. 251 × E.B. 438. The X^2 value indicated a good fit to a ratio of 1 homozygous two-rowed: 2 heterozygous: 1 homozygous six-rowed families, thus conforming the results obtained in the F_2 generation. Segregation within the 42 heterozygous families closely approximated a 1: 2: 1 monohybrid ratio.

In the crosses, E.B. 171 × E.B. 417 and E.B. 177 × E.B. 417, the F_2 genotypes could be classified into seven classes on the basis of their F_3 behaviour. Table I (*c*) presents the observed and the expected segregations on the genetic hypothesis outlined. There was general agreement between observed and expected data. The homozygous two-rowed classes were in excess of what was expected while the two-rowed: infertile intermedium segregating class showed a high deviation from the calculated in the cross E.B. 171 × E.B. 417. This may probably be due to the wrong classification of some families into the two-rowed group. Actually a family taken as homozygous two-rowed might have been segregating for two-rowed: infertile intermedium class. The homozygous intermedium families were observed to have 5–7% lateral florets fertile. All the plants classed as six-rowed in the F_2 bred true to that character.

(*b*) H. vulgare × H. deficiens *crosses*.—The inheritance of fertility of the lateral florets in *H. vulgare* × *H. deficiens* was studied in two crosses, *viz.*, K. 251 × E.B. 132 and C. 138–2 × E.B. 132, in the F_1, F_2 and F_3. The B_1 generation was also studied in K. 251 × E.B. 132. The varieties K. 251 and C. 138–2, which were used as the female parents, had the side florets fully fertile (six-rowed), while E.B. 132, the male parent, was a two-rowed *deficiens* type with the side florets very rudimentary. The F_1 and F_2 generations of these crosses were studied during two years. During 1956–57, the F_1 and F_2 plants were classified into two groups, *viz.*, two-rowed and six-rowed. In 1957–58, the development of the lateral florets was also taken into consideration, while classifying the segregating population. The observations on the parents, F_1, F_2, B_1 and F_3 generations are summarized in Tables II (*a*) and (*b*).

When only two groups, two-rowed and six-rowed, were taken into consideration, the F_1 was two-rowed and the F_2 segregation showed a good fit to a ratio of 3 two-rowed: 1 six-rowed in both the crosses. When development of the lateral florets was also taken into consideration, the F_1 plants were two-rowed, with the side florets slightly developed but all sterile. The lemma appendages of these florets were also rounded, like the two-rowed *distichon* variety (Pl. X, Fig. 2). In the F_2 generation, the plants could be grouped quite easily into three types, *viz.*, *deficiens*, intermediate like F_1 and six-rowed and closely approximated a 1: 2: 1 monohybrid ratio. The back cross to the *deficiens* parent gave a good fit to a ratio of 1 intermediate: 1 two-rowed *deficiens*, while the back cross to the six-rowed parent segregated in a 1: 1 ratio for intermediate and six-rowed.

In the F_3, large populations of individual families were grown to study their breeding behaviour. The data given in Table II (*b*)

TABLE II

Inheritance of fertility of the lateral florets between H. vulgare × H. deficiens *crosses*

(a) *Classification of parents, F_1, F_2 and B_1 generations*

Year of study	Material	Number of plants				X^2	P. value
		Two-rowed	Intermediate	Six-rowed	Total		
1956–57	*Cross: K. 251 × E.B. 132:*						
	K. 251	..	..	30	30		
	F_1	.. 15	..	..	15		
	F_2 observed	.. 140	..	55	195		
	F_2 expected (3:1)	.. 146·25	..	48·75	..	1·068	·50–·30
	E.B. 132	.. 30	..	..	30		
	Cross: C. 138–2 × E.B. 132:						
	C. 138–2	.. ..	..	28	28		
	F_1	.. 12	..	..	12		
	F_2 observed	.. 305	..	107	412		
	F_2 expected (3:1)	.. 309	..	103	..	0·207	·70–·50
	E.B. 132	.. 30	..	..	30		
1957–58	*Cross: K. 251 × E.B. 132:*						
	K. 251	.. ..	..	15	15		
	F_1	.. ..	7	..	7		
	F_1 × E.B. 132 observed	.. 21	31	..	52		
	F_1 × E.B. 132 expected (1:1)	.. 26	26	..	..	1·923	·20–·10
	F_1 × K. 251 observed	.. ..	53	51	104		
	F_1 × K. 251 expected (1:1)	.. ..	52	52	..	0·038	·90–·80
	F_2 observed	.. 148	301	163	612		
	F_2 expected (1:2:1)	.. 153	306	153	..	0·898	·70–·50
	E.B. 132	.. 15	..	..	15		
	Cross: C. 138–2 × E.B. 132:						
	C. 138–2	.. ..	..	37	37		
	F_1	.. ..	18	..	18		
	F_2 observed	.. 158	236	134	618		
	F_2 expected (1:2:1)	.. 154·5	309	154·5	..	3·734	·20–·10
	E.B. 132	.. 15	..	..	15		

(*b*) *Classification of* F_3 *families*

Material	Number of families				X^2	P. value
	Homozygous two-rowed	Segregating	Homozygous six-rowed	Total		
Cross: K. 251×E.B. 132						
F_3 observed	25	40	25	90		
F_3 expected (1:2:1)	22·5	45	22·5		1·11	·70–·50
Cross: C. 138–2×E.B. 132						
F_3 observed	14	47	19	80		
F_3 expected (1:2:1)	20	40	20		3·1	·30–·20

confirmed that this character was controlled by a single factor pair. All the plants classed as six-rowed in the F_2 bred true to this character. The families which were classified as "two-rowed" during 1956–57 segergated in a ratio of 1 homozygous two-rowed *deficiens*: 2 heterozygous two-rowed. Each heterozygous family further segregated in the ratio of 1 two-rowed *deficiens*: 2 intermediate: 1 six-rowed.

2. *Inheritance of hoods* vs *long awns*

Two crosses, K. 251×E.B. 132 and C. 138–2×E.B. 132, were studied in the F_1, F_2, F_3 and B_1 generations with regard to this character. The varieties, K. 251 and C. 138–2, had long awns on all the florets, while E.B. 132 had sessile hoods. The F_1 and F_2 generations of these crosses were studied during two years, *viz.*, 1956–57 and 1957–58. During 1957–58, the B_1 and F_3 generations were also studied. The results are given in Tables III (*a*) and (*b*).

The F_1 in both the crosses was hooded, though the hoods were borne on awns from one half to one inch in length (Pl. X, Fig. 2). In the F_2 generation sessile hooded, elevated hooded and fully long-awned types were obtained. In the case of the elevated hooded types, there was considerable variation in the length of the awns carrying these hoods, the length being from about $\frac{1}{4}$ inch to 2 inches (Pl. X, Fig. 3). The data based on the 3 characters, *viz.*, sessile hoods, elevated hoods and long awns did not fit any genetic ratios. However, when sessile and elevated hooded types were combined, the F_2 segregation gave a good fit to a ratio of 3 hooded: 1 long-awned during the year 1956–57, though the fit was not good in the year 1957–58. In one cross the awned types

TABLE III

Inheritance of hoods vs *long awns character*

(a) *Classification of parents, F_1, F_2 and B_1 generations*

Year of study	Material	Number of plants					X^2	P. value
		Hooded			Awned	Total		
		Sessile	Elevated	Total				
	Cross: K. 251 × E.B. 132							
1956–57	K. 251	..	..	..	35	35		
	F_1	..	13	13	..	13		
	F_2 observed	63	84	147	48	195		
	expected (3 : 1)	..	..	146·25	48·75	..	0·015	·95–·90
	E.B. 132	36	..	36	..	36		
	Cross: C. 138-2 × E.B. 132							
	C. 138-2	..	..	..	31	31		
	F_1	..	9	9	..	9		
	F_2 observed	114	199	313	101	414		
	F expected (3 : 1)	..	..	310·5	103·5	..	0·081	·80–·70
	E.B. 132	36	..	36	..	36		
	Cross: K. 251 × E.B. 132							
1957–58	K. 251	..	..	..	15	15		
	F_1	..	7	..	..	7		
	F_1 × K. 251 observed	..	47	47	57	101		
	expected (1 : 1)	..	..	52	52	..	0·961	·50–·30
	F_2 observed	299	132	431	181	612		
	expected (3 : 1)	..	..	459	153	..	6·832	<·01
	E.B. 132	15	..	15	..	15		
	Cross: C. 138-2 × E.B. 132							
	C. 138-2	..	..	..	37	37		
	F_1	..	18	18	..	18		
	F_2 observed	299	188	487	129	616		
	expected (3 : 1)	..	..	462	154	..	5·411	·65–·02
	E.B. 132	15	..	15	..	15		

TABLE III (*Contd.*)

(*b*) *classification of* F_3 *families*

Material	Number of families				X^2	P. value
	Homozygous hooded	Segregating	Homozygous long-awned	Total		
		Cross: K. 251×E.B. 132				
F_3 observed ..	27	43	20	90		
expected (1 : 2 : 1)	22·5	45	22·5		1·355	·70–·50
		Cross: C. 138–2×E.B. 132				
F_3 observed ..	18	41	21	80		
expected (1 : 2 : 1)	20	40	20	..	0·275	·90–·80

were more than the expected number, while in the other cross the awned types were less than the expected. The B_1 data showed that this character was controlled by one factor pair.

The segregation of this character was also studied in 90 F_3 families in K. 251×E.B. 132 and 80 F_3 families in C. 138–2×E.B. 132. The segregation of the families into homozygous hooded, segregating and homozygous awned was 27 : 43 : 20 in the first cross and 18 : 41 : 20 in the second cross. The segregation in each cross gave a good fit to a ratio of 1 : 2 : 1. As regards the breeding behaviour of these F_3 families, it was observed that all the forty-one homozygous long-awned families, in the two crosses taken together, were the progenies of long-awned F_2 plants. All the 45 families with sessile hoods were similarly derived F_2 plants that were classed as " sessile hooded". Out of 84 segregating families, 74 were the progenies of F_2 plants that had been classified as " elevated hooded". The remaining ten families, however, belonged to F_2 plants that had been classified as " sessile hooded". The classification of these ten F_2 plants was, perhaps, not strictly correct as the hoods might have been borne on very small tips of the lemma appendages and as such, the plants were perhaps not clearly distinguishable from truly sessile hooded plants.

3. *Inheritance of long* vs *short outer glume awns*

The mode of inheritance of this character was studied in five crosses, the long-awned parents being K. 251, C. 138–2, E.B. 171 and E. B.177, while the short-awned parents were E.B. 132, E.B. 417 and E.B. 438. The details of the observed segregations in the different generations are presented in Tables IV (*a*) and (*b*).

TABLE IV

Inheritance of long vs *short outer glume awns*

(a) classification of parents, F_1, F_2 and B_1 generations

Material	Number of plants			X^2	P. value
	Long-awned	Short-awned	Total		
Cross: E.B. 171×E.B. 417					
E.B. 171	24	..	24		
F_1	6	..	6		
F_1×E.B. 171	19	..	19		
F_2 observed	377	141	518		
F_2 expected (3 : 1) ..	388·5	129·5	..	1·362	·30–·20
E.B. 417	..	36	36		
Cross: E.B. 177×E.B. 417					
E.B. 177	36	..	36		
F_1	11	..	11		
F_2 observed	361	108	469		
F_2 expected (3 : 1) ..	351·75	117·25	..	0·972	·50–·30
Cross: K. 251×E.B. 438					
K. 251	28	..	28		
F_1	11	..	11		
F_2 observed	270	94	364		
F_2 expected (3 : 1) ..	273	91	..	0·131	·80–·70
E.B. 438	..	21	21		
Cross: K. 251×E.B. 132					
K. 251	15	..	15		
F_1	7	..	7		
F_1×E. 251	104	..	104		
F_1×E.B. 132 observed ..	27	25	52		
F_1×E.B. 132 expected (1 : 1)	26	26	..	0·076	·80–·70
F_2 observed	451	161	612		
F_2 expected (3 : 1) ..	459	153	..	0·557	·50–·30
E.B. 132	..	15	15		
Cross: C. 138–2×E.B. 132					
C. 138–2	37	..	37		
F_1	18	..	18		
F_2 observed	435	183	618		
F_2 expected (3 : 1) ..	463·5	154·5		7·009	< ·01
E.B. 132	..	15	15		

TABLE IV (*Contd.*)

(*b*) *Classification of* F_3 *families*

Material	Number of families				X^2	P. value
	Homozygous long-awned	Segregating (3 : 1)	Homozygous short-awned	Total		
Cross: E.B. 171×E.B. 417						
F_3 observed	33	43	24	100		
F_3 expected (1 : 2 : 1)	25	50	25	..	·358	·20–·10
Cross: E.B. 177×E.B. 417						
F_3 observed	25	45	21	91		
F_3 expected (1 : 2 : 1)	22·75	45·5	22·75	..	0·362	·90–·80
Cross: K. 251×E.B. 438						
F_3 observed	25	38	17	80		
F_3 expected (1 : 2 : 1)	20	40	20	..	3·3	·20–·10
Cross: K. 251×E.B. 132						
F_3 observed	22	44	23	89		
F_3 expected (1 : 2 : 1)	22·25	44·5	22·25	..	1·5	·50–·30
Cross: C. 138–2×E.B. 132						
F_3 observed	15	42	23	80		
F_3 expected (1 : 2 : 1)	20	40	20	..	3·0	·30–·20

The character of long awns was dominant over that of short awns in the F_1 in all the five crosses studied (Pl. X, Fig. 4). The segregation in the F_2 showed a good fit to a ratio of 3 : 1 for long-awned and short awned classes in all the crosses except C.138–2×E.B. 132. The back crosses with the long glume-awned parents had only long glume-awned plants, while the back cross with short glume-awned parents segregated in a 1 : 1 ratio of long glume-awned to short glume-awned plants. The segregation of F_3 families in all the five crosses showed a good fit to a ratio of 1 homozygous long-awned : 2 heterozygous : 1 homozygous short-awned families.

4. *Inheritance of broad* vs *narrow leaves*

The mode of inheritance of this character was studied in the cross K. 251 × E.B. 438, the broad-leaved parent being K. 251 while E.B. 438 had narrow leaves. The details of the segregations in the F_2 and F_3 generations are given in Tables V (*a*) and (*b*).

TABLE V

Inheritance of broad vs *narrow leaves in the cross K. 251 × E.B. 438*

(a) *Classification of parents, F_1 and F_2 generations*

Material	Number of plants			X^2	P. value
	Broad-leaved	Narrow-leaved	Total		
K. 251	28	..	28		
F_1	11	..	11		
F_2 observed ..	293	94	387		
F_2 expected (3 : 1) ..	290·25	96·75	..	0·104	·80–·70
E.B. 438	..	21	21		

(*b*) *Classification of F_3 families*

Material	Number of families				X^2	P. value
	Narrow-leaved	Segregating (3 : 1)	Broad-leaved	Total		
F_3 observed	20	38	22	80		
F_3 expected (1 : 2 : 1)	20	40	20	..	0·3	·90–·80

The F_1 showed dominance of broad leaves over narrow leaves. The F_2 segregation gave a good fit to a ratio of 3 : 1 for broad and narrow leaves. The segregation in the F_3 generation confirmed this ratio.

5. *Inheritance of early growth habit*

The cross K. 251 × E.B. 438 was studied to find out the mode of inheritance of early growth habit. The parent K. 251 had erect habit

of growth, while E.B. 438 was semi-spreading. The details of the F_2 and F_3 segregations are set out in Table VI (*a*) and (*b*) respectively.

TABLE VI

Inheritance of early growth habit in the cross K. 251 × E.B. 438

(a) *Classification of parents, F_1 and F_2 generations*

Material	Number of plants			X^2	P. value
	Semi-spreading	Erect	Total		
K. 251	..	11	11		
F_1	11	..	11		
F_2 observed	278	99	377		
F_2 expected (3 : 1) ..	282·75	94·25	..	0·399	·70–·50
E.B. 438	21	..	21		

(*b*) *Classification of F_3 families*

Material	Number of families				X^2	P. value
	Homozygous semi-spreading	Segregating	Homozygous erect	Total		
F_3 observed ..	8	23	8	39		
F_3 expected (1 : 2 : 1)	9·75	19·5	9·75	..	1·25	·70–·50

The semi-spreading habit of growth showed dominance over the erect habit in the F_1. In the F_2, some intergradations between the two classes were also observed. However, for interpretation of the data only two classes, *viz.*, erect and semi-spreading were taken into consideration. The data given in the above tables indicate that the segregation in the F_2 closely approximated a ratio of 3 semi-spreading: 1 erect. The F_3 data further confirmed that this character was controlled by a single factor.

6. *Inheritance of heading date*

The mode of inheritance of earliness, as represented by the number of days taken for heading, was studied in four crosses, *viz.*, K. 251 × E.B. 438, K. 251 × E.B. 145, C. 138–2 × E.B. 145 and N.P. 13 × E.B. 145. The cross K. 251 × E.B. 438 was studied at Delhi during the year 1957–58 through the F_1, F_2 and F_3 generations. The cross K. 251 × E.B. 145 was studied at two locations, *viz.*, Delhi and Wellington (Nilgiri Hills), during the year 1956–57 through F_1 and F_2 generations. C. 138–2 × E.B. 145 and N.P. 13 × E.B. 145 were studied in the F_1 and F_2 generations at Wellington only during 1956–57.

The parents K. 251, C. 138–2 and N.P. 13 were early types, the range of heading date varying from 90–95 days, while E.B. 145 and E.B. 438 were mid-late varieties taking about 105 and 110 days respectively for heading. The heading dates of the parents, F_1, F_2 and F_3 generations in the crosses grown at Delhi were recorded on individual plant basis. The frequency distribution (class interval of 3 days) of the parents, F_1 and F_2 generations of K. 251 × E.B. 438 and K. 251 × E.B. 145 are given in Table VII.

The F_1 in both the crosses was inclined towards the early parent, K. 251, as compared to the mean of the two parents, indicating almost complete dominance of earliness. The relatively high C.V. in the F_1 of K. 251 × E.B. 438 cross was due to the small number of the plants in this generation and the fact that three out of a total of 11 plants came into ear much earlier than the other 8. The F_2 means of both the crosses also showed a shift towards the earlier parent which definitely supported the assumption that earliness was dominant. The coefficient of variation in F_2 increased considerably over the parents in both the crosses. This was to be expected, as under normal conditions without any linkage the greatest amount of variability should be present in F_2. The range of segregation in F_2 almost covered the ranges of distribution of both early and late parents. Thus the parental types were recovered in a comparatively small F_2 population.

The distributions in F_2 and F_3 generations were divided into two populations, *viz.*, early and late, as suggested by Frey (1954). For this purpose the mid-point between the nearest classes of the two parents of a cross was taken as the dividing line between early and late segregates. The distributions of the F_2 and F_3 populations showing segregation for heading date and X^2 tests for goodness of fit are given in Tables VIII and IX respectively.

The segregations in the F_2 of both the crosses gave good fit to a ratio of 3 early : 1 late showing that heading date was inherited on the basis of a simple monohybrid ratio. In the F_3 generation of K. 251 × E.B. 438, three types of families could be distinguished quite easily; (i) breeding true for earliness, (ii) segregating and (iii) breeding true for lateness. The X^2 value gave a good fit to a ratio of 1 : 2 : 1 confirming the operation of a single factor pair for heading date.

Frequency distribution of the parents, F_1 and F_2 plants of the crosses K. 251×E.B. 145 and K. 251×E.B. 438 by number of days from sowing to heading (class interval of 3 days)

Material	Class centres												Total	Mean	C.V.
	83	86	89	92	95	98	101	104	107	110	113	116			
Cross: K. 251×E.B. 145 (1956–57)															
K. 251 ..				1	15	10							26	96·0±0·3310	1·75
F_1 ..						4							4	98·0	
F_2 ..				9	200	204	82	48	3				546	97·8±0·1272	3·04
E.B. 145							4	20					24	103·5±0·2332	1·1
Cross: K. 251×E.B. 438 (1957–58)															
K. 251 ..		3	7	15	3								28	90·9±0·4821	2·72
F_1 ..		3	..	..	5	3							11	93·4±1·4788	5·25
F_2 ..	2	12	52	54	101	41	49	38	17	3	..	1	370	96·1±0·2948	5·91
E.B. 438									3	7	4	7	21	112·1±0·7218	2·94

TABLE VIII

Segregation of the F_2 population into early and late plants

Material	Number of plants			X^2	P. value
	Early	Late	Total		
Cross: K. 251×E.B. 145					
F_2 observed ..	413	133	546		
F_2 expected (3:1) ..	409·5	136·5	..	0·1196	·80–·70
Cross: K. 251×E.B. 438					
F_2 observed ..	286	83	369		
F_2 expected (3:1) ..	276·75	92·25	..	1·236	·30–·20

TABLE IX

Segregation for heading date in the F_3 families of the cross K. 251×E.B. 438

Material	Number of families				X^2	P. value
	Homozygous early	Segregating	Homozygous late	Total		
F_3 observed ..	26	40	14	80		
F_3 expected (1:2:1) ..	20	40	20	..	3·6	·20–·10

The crosses K. 251×E.B. 145, C. 138–2×E.B. 145 and N.P. 13×E.B. 145 were studied at Wellington in the F_1 and F_2 generations along with the parents during the year 1956–57. It is of interest to note that E.B. 145 showed differential response to location with regard to its heading date. This variety, when compared with the early heading varieties, K. 251, C. 138–2 and N.P. 13, headed 8–10 days later at Delhi, while at Wellington, E.B. 145 headed nearly 25 days later than the other three varieties just mentioned. The F_1 in all the three crosses showed dominance of earliness. The F_2 population could be distinctly classified into two groups, *viz.*, early and late like the parental types. The data are set out in Table X.

TABLE X

Segregation of the F_2 population for heading date (Material raised at Wellington)

Material	Number of plants			X^2	P. value
	Early	Late	Total		
Cross: K. 251×E.B. 145					
F_2 observed ..	286	92	378		
F_2 expected (3:1) ..	283·5	94·5	..	0·881	·50–·30
Cross: C. 138–2×E.B. 145					
F_2 observed ..	259	75	334		
F_2 expected (3:1) ..	250·5	83·5	..	1·153	·30–·20
Cross: N.P. 13×E.B. 145					
F_2 observed ..	264	96	360		
F_2 expected (3:1) ..	270	90	..	0·533	·50–·30

A perusal of Table X clearly shows that the F_2 segregations observed at Wellington could be explained by assuming the operation of one gene pair. The cross K. 251×E.B. 145 was studied at two locations. The data indicated that heading date was controlled by one gene at both the locations.

DISCUSSION

The data on the fertility of the lateral florets have given indications of two distinct types of segregation in the *H. vulgare×distichon* crosses. In the F_1 of the cross K. 251×E.B. 438 the lateral florets had small tips and produced two to three grains per ear. The F_2 segregation showed a simple monohybrid ratio of 1 six-rowed: 2 infertile intermediate: 1 two-rowed forms. The F_3 segregations confirmed this ratio, the F_2 plants classified as infertile intermediates having been observed to be heterozygous in the F_3 generation, while the two-rowed and the six-rowed types bred true to those characters respectively. Biffen (1907), Thatcher (1912), Gaines (1917), Engledow (1920, 1921), Fraser (1921), Griffee (1923), Tedin and Tedin (1926), Robertson (1929), Buckley (1930), Daane (1931), Bose *et al.* (1937) and others reported similar results with crosses of *H. vulgare* with *H. distichon*.

Engledow (1920) found more than three classes with regard to the fertility of the lateral florets in the F_2 generation. Ubisch (1917),

Harlan and Hayes (1920), Griffee (1925), Barbacki (1929), Robertson (1929, 1933), Leonard (1942), Woodward (1949) among others explained the fertility of the lateral florets on the basis of a two-factor difference. Ubisch (1917) assumed that the expression of *Z* was responsible for the two-rowed condition and that the gene *W* produced the intermedium type. On this hypothesis, the two-rowed parent carried the intermedium factor in a hypostatic condition. Harlan and Hayes (1920) also obtained true breeding intermedium types in the F_3 generation and explained their results by assuming that the six-rowed variety carried two factors, one for the six-rowed condition and the other which was responsible for the intermedium condition and hypostatic to the former. This explanation is now generally accepted. The results of the present studies are in accord with the findings of Harlan and Hayes (1920). The F_1 of the crosses E.B. 171 × E.B. 417 and E.B. 177 × E.B. 417 had highly fertile lateral florets (90–95%) with intermediate awns, 2–4 cm. long. The F_2 population showed five different types for this character, *viz.*, two-rowed, fertile intermediate, infertile intermediate, partly fertile intermedium and six-rowed. The data gave a good fit to a ratio of 9 intermediums and intermediates: 3 two-rowed: 4 six-rowed types. On the basis of the segregations observed in the F_3 generation, seven genotypes could be easily classified. Homozygous partly fertile intermedium families with two to three grains per ear in the lateral florets were observed in the F_3 generation.

The inheritance of the fertility of the lateral florets in the crosses of *H. vulgare* with *H. deficiens* was studied in K. 251 × E.B. 132 and C. 138–2 × E.B. 132. The F_1 in these crosses was weak two-rowed. The lateral florets were slightly developed, sterile and had rounded appendages like the *distichon* type. The F_2 segregations could be easily explained on the basis of a monohybrid ratio of 1 *deficiens*: 2 intermediate: 1 six-rowed. The F_3 segregations confirmed this finding. No family breeding true to the two-rowed *distichon* type was observed. Biffen (1907), Engledow (1920), Hor (1924), Gillis (1926), Griffee (1925), Powers (1936), Leonard (1942), Woodward (1949) and others reported similar results. Ubisch (1923), however, presented some data which were contradictory to this assumption. From a cross between *deficiens* and six-rowed types, normal two-rowed plants were obtained in the ratio of 9 two-rowed: 3 six-rowed: 4 *deficiens*. It was assumed that two dominant factors, *Z* and *D*, produced the two-rowed type, *D* alone (with *z*) gave rise to the six-rowed condition and *Z* or *z* with *d* gave rise to the *deficiens* type. Biffen (1907), Engledow (1920), Hor (1924) and Woodward (1947, 1949) concluded that *deficiens*, *distichon* and *vulgare* formed a series of multiple alleles, dominance operating in the same order. These types have been designated as V^tV^t for *deficiens*, *VV* for *distichon* and *v v* for *vulgare*. Leonard (1942) and Woodward (1947) concluded that the fertile, infertile and non-intermedium types were differentiated by genes belonging to a multiple series, designated as I^hI^h, *II*, *ii* respectively and that I^h, *I* and *i* alleles were hypostatic to *vv* (six-rowed). Likewise, the V^tV^t factor for *deficiens* was epistatic to the I^h, *I*, *i* genes.

According to the scheme postulated by Woodward (1949) six-rowed types would be *vv* I^hI^h or *vv II* or *vv ii*; *distichon*, *VV ii*; *intermediums*, *VV* I^hI^h or *VV II* and *deficiens*, V^tV^t I^hI^h, V^tV^t *ii* or V^tV^t *II*. The results obtained in the present studies give support to the theory of allelic series for non-six-rowed *vs* six-rowed and intermedium *vs* non-intermedium types. The *distichon* parents, E.B. 417 and E.B. 438, would have the genotype *VV ii*. K. 251, a six-rowed variety, when crossed with the *VV ii* genotype, showed in the F_1 infertile lateral florets which were only slightly developed and had small beaks on them, indicating the dominance of the *V* factor. The segregations in the F_2 and F_3 generations confirmed that K. 251 was homozygous for the recessive *ii* factor and as such its genotype would be *vv ii*. The six-rowed types, E.B. 171 and E.B. 177, gave indications of their genotypes being *vv* I^hI^h. When they were crossed with the *VV ii* genotype the F_1 was highly fertile intermediate with fairly long-awned laterals. The segregations in F_2 and F_3 were what should be expected on this assumption. The crosses of *H. vulgare* with *H. deficiens* could not be classified for their fertility genes, because like the six-rowed types *vv*, the *deficiens* V^tV^t is also epistatic to the I^h, *I* and *i* series and since all the plants would carry either *v* or V^t the fertility genes would not be able to express themselves. The genotype of the *deficiens* type, E.B. 132 in regard to the fertility genes can be determined by crossing it with *VV ii*. A cross between E.B. 132 and *VV ii* is, therefore, under study for this purpose.

A number of workers reported that the F_1 in crosses between hooded and awned forms was hooded, although in many cases more or less intermediate. The F_2 segregation was readily explained on a monohybrid ratio of 3 hooded: 1 awned (Biffen, 1907; Thatcher, 1912; Gaines, 1917; Kezer and Boyack, 1918; Fraser, 1921; Hor, 1924; Waterhouse, 1927; Hayes and Garber, 1927; Robertson, 1929; Buckley, 1930; Daane, 1931; Litzenberger and Green, 1951 and others). Biffen (1907) studied seven crosses between hooded and awned varieties and obtained all hooded individuals in the F_1. In two of the crosses, however, the hoods were borne on awns one half to four inches in length. The F_2 segregated into 3 hooded: 1 awned. In the case of the awned-hooded heterozygote the F_2 showed considerable variation in the length of the awned-hood but no indications could be detected of segregation into individuals with sessile hoods, awned-hoods and true awns only. In the present studies, the F_1's of crosses between sessile hooded and fully long-awned types were observed to be elevated hooded. In the F_2, three classes, *viz.*, sessile hooded, elevated hooded and fully awned types were obtained. In the elevated hooded types, however, there was a wide range of variation in the elevation of the hoods. In some plants hoods were observed on awns 5–6 cm. in length, while in others they were borne on awns only $\frac{1}{4}$ cm. in length. Glinyany (1937) reported the presence of hoods as well as awns on one and the same ear in some cases. Such a condition was not found in any plant in the present studies. If a plant was long-awned it was uniformly long awned. Similar was the case with elevated hooded and sessile hooded plants. Taking sessile and elevated hooded types together in one group, the

F_2 segregation gave indications of a one factor difference, the ratio being 3 hooded: 1 long-awned. In the F_3 generation, sessile and fully long-awned types bred true to these characters respectively and the elevated hooded types were heterozygous. Takahashi and Iteno (1952) concluded that normal hooded (*K*). elevated hooded (K^e) and long awns (*k*) were controlled by an allelomorphic series of genes.

Thatcher (1916) in a cross between an awnless and a hooded variety found the F_1 to have reduced hoods; in the F_2 there was an almost continuous series of development of awns and hoods. He explained the results by assuming the operation of two genes. One dominant factor *H* produced hoods and its recessive resulted in awns. A second factor in the dominant condition suppressed H, two doses of the dominant alleles being more effective than one in suppressing *H* and *h*. Myler (1942) concluded that two dominant awned factors, *LkLk*, $Lk_1\ Lk_1$ besides the factor *KK* for hoods must be present for the development of hooded plants. Long-awned plants carried both dominant awn factors, while short awned plants had *lk* in recessive and Lk_1 in dominant condition. Woodward and Rasmussen (1957) indicated that one or more dominant genes from each gene pair, *KK LkLk*, must be present in order for hoods to develop. Long awns developed when *k* was in the homozygous recessive condition and the *Lk* gene either homozygous or heterozygous. Short awns appeared when *lk* was homozygous recessive. The genotype of the long-awned type was, therefore, *kk LkLk* and that of short-awned types *KK lklk*. Albrechtsen (1957) classified sessile hoods as having the genotype $KK\ K_2K_2$; median hoods, $Kk\ K_2K_2$; extremely elevated hoods with mixed awns as regards length, $KK\ K_2k_2$ and $Kk\ K_2k_2$; long awns, $KK\ k_2k_2$ and $Kk\ k_2k_2$ and short awns, $kk\ K_2K_2$, $kk\ K_2k_2$ and $kk\ k_2k_2$. Taking into consideration the genotypic classification postulated by Albrechtsen (1957) it is to be concluded that the long-awned parents, K. 251 and C. 138–2 have the genotypes $KK\ k_2k_2$, while the sessile hooded variety, E.B. 132, had the genotype, $KK\ K_2K_2$. The F_1 on this assumption was $KK\ K_2k_2$, which was elevated hooded. The wide variation in the degree of elevation of the hoods further suggested that there were, perhaps, some modifying factors apart from the major one for this character.

The mode of inheritance of long *vs* short outer glume awns was studied in five crosses. The data indicated that this character was controlled by one factor pair, the long outer glume awns being dominant over short awns in the F_1. This character was probably first studied by Hor (1924). In a cross between a variety with outer glume awns as long as those of lemma and one with short-awned outer glumes, the F_1 was intermediate. The F_2 segregation was in the ratio of 1 long-awned: 2 intermediate: 1 short awned. Litzenberger and Green (1951) studied the inheritance of long and short awns (lemma appendages) in crosses of fully short-awned × long-awned varieties and observed a single factor difference, the long awns being apparently completely dominant over short awns.

In the F_1 of the cross K. 251 × E.B. 417, the broad leaves of K. 251 were dominant over the narrow leaves of E.B. 417. The segregations

in the F_2 and F_3 generations confirmed that the production of broad leaves *vs* narrow leaves was controlled by a single factor pair. Miyazawa (1929) found that the width of the leaf was intermediate in hybrids between narrow and broad-leaved types. In the F_2 the segregation seemed to conform to a 1:2:1 ratio. No other work seems to have been done on the inheritance of this character in barley.

The mode of inheritance of early growth habit was studied in the cross K. 251 × E.B. 438. The F_1 showed dominance of the semi-spreading habit of E.B. 438 over the erect habit of K. 251. The segregation in the F_2 and F_3 generations clearly indicated that this character was controlled by a single factor difference. E.B. 438 was assumed to carry one dominant gene for semi-spreading type while K. 251 had its allele in a recessive condition for erectness. The inheritance of early growth habit does not seem to have been studied in barley by previous workers, though much work was done in regard to the mode of inheritance of spring *vs* winter habit. Takahashi (1924, 1925), Schiemann (1925), Tschermak (1923, 1927) and others reported monofactorial differences. Gaines (1917) interpreted the genetics of winter habit on a two-factor basis by assuming that one of the varieties had dominant genes for winter type but that their action was suppressed by inhibitor genes. Li (1932) postulated a dominant factor *S* for the winter type and an inhibitor *I* for the spring type. Tokhtuyev (1940) observed that the spring habit was dominant in six crosses and winter habit was dominant in one cross studied by him. In the F_2, the six crosses gave a preponderance of spring types and one gave a 3:1 ratio of winter: spring. Hoffmann (1944) observed this character to be controlled by an allelic series with dominance of the spring type. Takahashi and Yasuda (1956) concluded that three major genes, *sh*, Sh_2 and Sh_3 were responsible for the spring habit, any one of which or any combination of which determined spring habit. Winter habit was only expressed by $Sh\ Sh\ sh_2\ sh_2\ sh_3\ sh_3$. They further observed that a series of multiple alleles at the locus sh_2 was responsible for intergrading between spring and winter habits, an allele for the higher degree of spring habit being dominant over alleles for lower degrees of spring habit.

The phenotypic expression of a quantitative character such as earliness may be considered as a result of two interacting factors, the genotype and the environment. Bell (1939) stressed the relationship between physiology, heredity and environment in the expression of earliness. He found the light requirement to be an exceedingly important factor in determining earliness in barley. For instance, a plant which was early in one area might react quite differently in another area where light intensity and duration differed. In the present studies, the mode of inheritance of heading date in the crosses involving early and medium-late varieties was studied at two locations, *viz.*, Delhi and Wellington (Nilgiris). Two crosses were studied at Delhi, and three crosses were studied at Wellington. One cross, K. 251 × E.B. 145, was common at both the locations. It is of interest to note that E.B. 145 showed a differential response to the location with regard to its heading date. At Delhi, this variety took about 10 days more for heading when

compared with early heading varieties, K. 251, C. 138–2 and N.P. 13, while at Wellington it showed a difference of about 25 days in its heading date when compared with K. 251. As regards the mode of inheritance, the data obtained at both the locations clearly indicated the dominance of earliness in the F_1. The parental types might be considered to have been recovered in the F_2 in view of the limited number of F_2 plants grown. The segregations in the F_2 and F_3 generations were easily explained on the assumption of the operation of a single gene difference. The cross K. 251 × E.B. 145 was studied at both the locations. It is significant to note that despite the fluctuations in the environmental conditions, the F_2 segregation was in the ratio of 3 early : 1 late at both the locations. This clearly indicated that the nature of inheritance of heading date was not influenced by the environment. Griffee (1925), Mackie (1926), Fiuzat and Atkins (1953) reported earliness to be dominant and determined by a single factor difference. Neatby (1926, 1929), Huber (1929), Johnston (1934), Johnston and Aamodt (1935), Chin (1941) concluded that earliness was dependent on two or more gene pairs in some crosses. Hehn (1948) found earliness to be determined by one, two or three genes depending on the varieties crossed. Harlan and Martini (1929) in a study of 351 F_1 hybrids involving 27 parents, showed that whether earliness was dominant or not, the degree of earliness and lateness depended upon the particular varieties used as parents. Johnson and Paul (1958) hypothesized that parents in each late × early cross differed by additive, increaser alleles at two loci, giving $a_ia_ib_ib_i \times$ *aabb*. Theoretically such a cross produced six F_2 breeding types, *viz.*, late, intermediate and early homozygotes, and late, intermediate and early heterozygotes; the ratio being 1 : 2 : 1 : 4 : 4 : 4. Wilson (1907) conducted one of the first genetic studies on early maturity and indicated that earliness was recessive to lateness. Frey (1954) also observed late condition to be dominant over earliness in the F_1 and explained his results on one and two factor differences in the crosses studied by him.

Summary

The mode of inheritance of the fertility of the lateral florets, in *H. vulgare* × *H. distichon* and *H. vulgare* × *H. deficiens* crosses, hoods (sessile) *vs* long awns, long *vs* short outer glume awns, leaf shape, early growth habit and heading date was studied in a number of crosses in the F_1, F_2 and F_3 generations. In some crosses, B_1 generation was also studied.

In the crosses of *H. vulgare* with *H. distichon*, two types of segregations were observed. In the cross, K. 251 × E.B. 438, the segregation was explained on a single gene difference while in the crosses, E.B. 171 × E.B. 417 and E.B. 177 × E.B. 417, fixed partially fertile intermediums were observed in the F_3 and the segregation was explained by assuming a two gene difference. E.B. 417 and E.B. 438 were assumed to have the genotype *VV ii*, K. 251 had the genotype *vv ii* while E.B. 171 and E.B. 177 carried the *vv* I^hI^h genotype.

In the crosses of *H. vulgare* with *H. deficiens*, the F_1 was weak two-rowed. The F_2 and F_3 segregations showed the operation of a single gene pair.

Two crosses, K. 251 × E.B. 132 and C. 138–2 × E.B. 132, were studied for sessile hoods *vs* long-awned type. The F_1 was elevated hooded. The segregations in the F_2 and F_3 generations showed that this character was controlled by a single gene pair. In addition, some modifier genes seemed to control awn length in the segregating population. The long-awned parents, K. 251 and C. 138–2, were assumed to have the genotype $KK\,k_2k_2$, while the sessile-hooded variety, E.B. 132, was regarded as $KK\,K_2K_2$.

The mode of inheritance of long *vs* short outer glume awns was studied in five crosses. This character was observed to be controlled by a single gene difference, the long-awned condition being dominant in the F_1.

The characters broad *vs* narrow leaves, semi-spreading *vs* erect types of early growth habit and heading date were also observed to be controlled each by a single gene difference, the F_1 showing the dominance of broad leaves, semi-spreading habit and early heading date.

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We are grateful to Dr. B. P. Pal, Director, Indian Agricultural Research Institute, for his keen interest in this study.

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* Originals not seen.

EXPLANATION OF PLATE X

FIG. 1. The fertility of the lateral florets in the crosses of *H. vulgare* (six-rowed) with *H. distichon* (two-rowed) forms.

(A) Two-rowed parent. (B) Six-rowed parent. (C) F_1, infertile intermediate:—The lateral florets are tipped and partially fertile (2–3 grains per ear). (D) F_1, Fertile intermediate:—the lateral florets are highly fertile (90–95%) and bear awns about 4 cm. long.

FIG. 2. The fertility of the lateral florets in the crosses of *H. vulgare* (six-rowed) with *H. deficiens* (two-rowed). (A) Two-rowed parent. (B) Six-rowed parent. (C) The F_1 ear is weak two-rowed. The lateral florets are slightly developed but infertile. The lemma appendages are also rounded. The same figure shows the cross between hooded (Sessile) × long-awned varieties. (A) The sessile hooded parent. (B) The long-awned parent. (C) the F_1 is elevated hooded. The hoods are borne on awns about two cm. in length.

FIG. 3. Sessile hooded, fully long-awned and elevated hooded forms with different degrees of elevation of the hoods, in the segregating F_2 population.

FIG. 4. A cross between long *vs* short outer glume awned varieties. (A) Long-awned parent. (B) Short-awned parent. (C) The F_1 is long-awned.

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FIGS. 1–4

A CONTRIBUTION TO THE STUDY OF AMARANTHACEAE

Achyranthes aspera var. *prophyristachya* Hook.f.

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The anatomy of a few species of genus *Achyranthes* has been investigated previously by Dastur (1925), Gupta (1934) and Joshi (1931, 1934, 1951). This paper describes the morphology and anatomy of *A. aspera* var. *prophyristachya* Hook.f. which is a recent inclusion in the flora of Bombay and Salsette Islands. This plant has been studied with a view to compare the structure of this plant with those previously studied by other workers and to throw light on the abnormalities formed in the stem of any member of *Amaranthaceæ* and *Chenopodiaceæ*.

Material and Methods

Plants were collected locally from Bombay and Salsette Islands as well as from Mahableshwar. The observations have been made from free-hand sections of stems stained with safranin and mounted in glycerine.

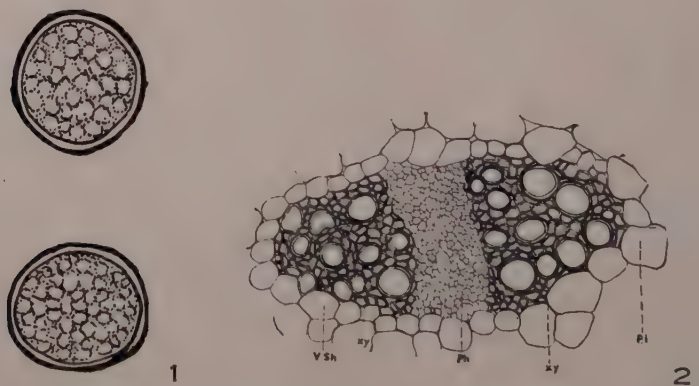
Distribution and Habitat

They are very common all along the footpath in the Dang Forest. Recently this variety is covering a fair space on Mumbra and Boriveli Hills. It reaches a height of about 60–130 cm. at Bombay, but the maximum height of 200 cm. is recorded at Mahableshwar. The plant flourishes well on hard soil. The ecological habits of the plant are such that it appears that *A. aspera* var. *prophyristachya* is heading from mesophytic to xerophytic group.

Morphology

Achyranthes aspera var. *prophyristachya* is an annual, erect herbaceous plant. The plant appears greenish-pink in colouration and usually attains 60–130 cm. height. The stem is 2–3·7 mm. thick at the base and is long and angular with shallow grooves. The grooves run parallel all along the main axis and seem to appear continuous from internode to internode. The nodal zones show a pair of lateral, opposite branches. These are rigid, ascending, angular, glabrous or sometimes sparingly pubescent. These branches terminate into inflorescence. Leaves are simple, opposite, and 6–10×2·5–3·6 cm. long.

They are linear to lanceolate to ovate, membranous, entire with acuminate apex and glabrous on both the surfaces. The petiole is long and exstipulate. The spike is terminal or axillary, long, slender and weak. Flowering and fruiting period is September to March. Flowers are greenish with purple tinge and they are larger than those of *A. aspera* L. The flowers are actinomorphic, bisexual and sessile. The bracteoles are 2, linear, more or less acuminate at the tip with a broad saccate hard base. Calyx are of 5 lobes, membranous with a broad base. They are ovate—lanceolate or ovate—oblong, with the spiny tips. Stamens are 5, filamentous and connected at the base forming a cup. This cup is fringed at the tip with a number of hair-like projections. Anthers are " H-shaped", and yellowish in colour. The filaments are attached to the centre of the connective. Pollen grains are round, partly spiny with yellowish minute rounded grain-like bodies in the cavity. Some of these are arranged on the inner side of the intine (Text-Fig. 1). Ovary is superior with a terminal style and a capitate stigma. There is a single pendulous ovule. The fruit is an utricle with a persistent style covered over by a persistent hard, brown calyx. There is a single seed sub-cylindrical blackish brown in colouration.



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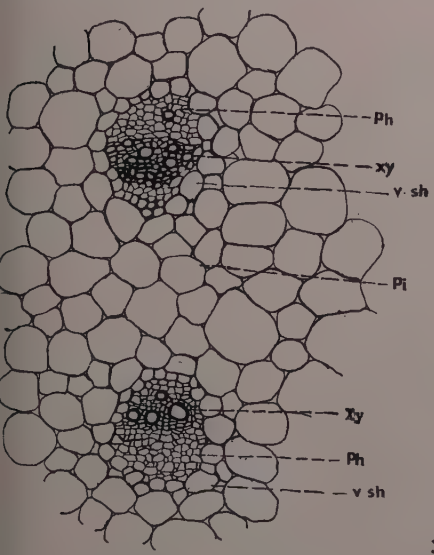
TEXT-FIGS. 1–2.—Fig. 1. Visible surfaces of Pollen grains. ×880. Fig. 2. T.S. Stem of showing amphixylic vascular strand (*V.Sh.*, Vascular sheath; *X.*, Xylem; *Ph.*, Phloem; *Pi.*, Pith), × 133.

ANATOMY

T.S. of a young internode (Text-Fig. 4) shows a number of ridges and furrows. Long tapering, multicellular epidermal hairs are more at the ridges. The epidermal cells are tabular, small and compact, their outer and the lateral walls are partly thickened and lignified. Angular collenchyma is confined to ridges and the chlorenchyma to the furrows. The development of collenchyma is well marked below the ridges. The cortex consists of thin-walled, parenchymatous cells with very few intercellular spaces. The endodermis is very distinct nd is characterised by thin-walled elongated cells. The pericycle

is made up of fibrous and non-fibrous cells. The vascular zone shows broad medullary ray due to the feeble development of primary vascular bundles. The pith cells are isodiametric and thin-walled in nature, showing two medullary vascular bundles. These medullary vascular bundles lie opposite to each other and they are well developed, collateral, conjoint, endarch and closed. The development of xylem and phloem tissues in these bundles is more or less the same in amount. Each of these bundles is enclosed by a parenchymatous sheath. These two free medullary vascular bundles are found only in 4–5 upper internodes of the flowering spikes, but below these internodes they run together and unite with each other to form a single strand at the centre. This may be described as a "double or a single amphixylic type". The pith and the cortical cells show the presence of calcium carbonate crystals (Text-Figs. 2 and 3).



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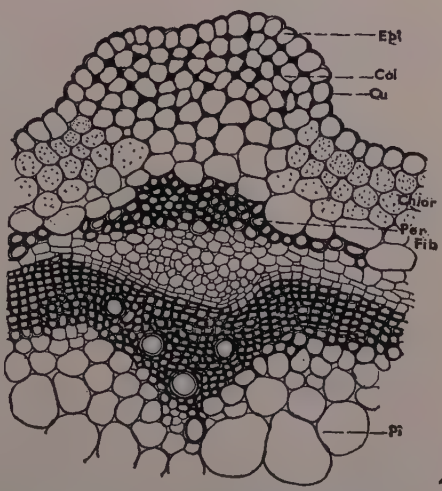

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TEXT-FIGS. 3–4. Fig. 3. T.S. of Stem, showing the two medullary vascular bundles in pith. (*Ph.*, phloem; *Xy.*, xylem; *V.Sh.*, Vascular Sheath) ×92. Fig. 4. T.S. of Stem. (*Epi.*, epidermis; *Col.*, Collenchyma; *Chlor.*, Chlorenchyma; *Per. Fib.*, pericycle fibres; *Pi.*, pith), ×200.

DISCUSSION

Wilson says: "Of all the departures from normal structure in the dicot stem, the medullary bundles is one of the most striking". Metcalfe and Chalk, mention the occurrence of medullary bundles in 38 families of dicotyledons (Vol. II, p. 1342). The presence of medullary bundles in such a large number of more or less unrelated families (including some of the most primitive, like Ranunculaceæ, Nepanthaceæ and Saxifragaceæ, as well as some of the most advanced, like Compositæ, Convolvulaceæ, Campanulaceæ and Umbelliferæ) renders it difficult to elaborate a phylogenetic interpretation of this

feature. As recorded by the present writer, there is an undeniable structural resemblance in *Achyranthes aspera* var. *prophyristachya* and other species of the Genus *Achyranthes*. One of the most important anatomical features in *A. aspera* var. *prophyristachya* Hook.f., is the presence of 2 free medullary vascular bundles in 4–5 upper internodal zones. The anatomy of these internodes bring this species in line with the other, *viz.*, *A. bidentata*, *A. argentea* and *A. crispa*. But the observations made to ascertain the behaviour of these medullary vascular bundles from internode to internode show that they touch each other and this condition is similar to that of *A. aspera* collected at Lahore (Joshi, 1934) but partly differs with those plants collected at Bombay and Calcutta.

The fusion of the two medullary vascular bundles of stem axis is one of the most important anatomical diagnostic character to separate this variety from *A. aspera* L. growing at Bombay. According to Joshi (1951) "It is quite clear the occurrence of two free medullary vascular bundles throughout the length of an internode is a primitive condition; and their fusion in the middle of an internode to form a single strand is a later and derived condition".

Another point of great interest in the anatomy of *A. aspera* var. *prophyristachya* is that both the medullary vascular bundles are collateral and conjoint and they remain so throughout their course in the stem axis. There is no such condition in this plant as observed by Gupta (1934) in *A. aspera* L. "that of the two medullary vascular bundles one is normal and other is amphixylic".

The medullary vascular bundles in *A. aspera* var. *prophyristachya* contain almost the same amount of xylem and phloem. No mention is made about this feature in *A. aspera* either by Dastur (1925), Gupta (1934) or Joshi (1931, 1934, 1951). It seems reasonable to suppose that since *A. aspera* var. *prophyristachya* Hook. f. has a larger growth, the demands made upon the conducting system are so great that they cannot be met by the normal ring of vascular bundles. It is quite possible that these internal bundles are formed in response to this demand with a fair development of phloem elements.

The medullary vascular bundles in *A. aspera* var. *prophyristachya* are completely enclosed by a parenchymatous bundles sheath. This is to give a better mechanical support to the medullary vascular bundles. There is no reference regarding the vascular sheath in any species of *Achyranthes*.

Morphologically this variety shows many differences with that of *A. aspera* L., *viz.*, the leaves of *A. aspera* var. *prophyristachya* are linear to lanceolate while in *A. aspera* L. they are broadly ovate.

Another striking morphological feature in *A. aspera* var. *prophyristachya* is the development of a long but slender inflorescence axis, while in *A. aspera* it is stout and strong. The flowers of *A. aspera* var. *prophyristachya* are larger than those of *A. aspera* L.

In *A. aspera* var. *prophyristachya* there are many round yellowish bodies in the pollen grain while in *A. aspera* there are 8–10 pinkish bodies.

Summary

Achyranthes aspera var. *prophyristachya* presents a number of external features, *viz.*, leaves linear to lanceolate, and inflorescence axis is long and slender. Flowers are larger than those of *A. aspera.* Pollen grains are spiny and the fruit is a cylindrical utricle.

Internally in *A. aspera* var. *prophyristachya* there appear 2, free medullary vascular bundles only in 4–5 upper internodes; later on they fuse to form amphixylic strand at the centre. Each medullary vascular bundle is well protected by vascular sheath. The cortex and pith show the presence of calcium crystals.

Acknowledgement

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EFFECT OF CARBON AND NITROGEN NUTRITION ON GROWTH AND SPORULATION OF *COLLETOTRICHUM CAPSICI* (SYD.) BUTLER AND BISBY

By A. P. Misra and M. Mahmood

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(Received for publication on March 16, 1959)

There is considerable diversity in the ability of fungi to use various carbohydrate and nitrogen sources. Grewal (1957) studied the carbohydrate metabolism of three anthracnose fungi, *viz.*, *Glaeosporium musarum*, *G. papayae* and *Colletotrichum papayae* and found that lactose, sucrose, glucose and galactose supported good mycelial growth. Thind and Randhawa (1957), using 42 carbohydrates in liquid cultures, found best growth of *Colletotrichum capsici* on dextrose, sucrose and maltose, good growth on fructose and poor or no growth on rest of the carbon sources. In studies on nitrogen nutrition these authors noted best growth of the fungus on alanine, valine, arginine and urea.

The present paper deals with the response of *C. capsici* to several sources of carbon and nitrogen at different concentrations and to ratios of lactose and asparagine which gave maximum growth. Observations on the effect of various treatments on sporulation of the organism have also been included.

Material and Methods

Czapek's medium (found in earlier experiments to be the best for growth and sporulation of *C. capsici*) was taken as the basal medium. The carbohydrates and nitrogenous compounds were incorporated separately in the medium so as to supply the same amounts of carbon and nitrogen contained in Czapek's medium. The pH of the medium in all cases was adjusted to 5·0. Twenty-five ml. of the medium were pipetted out into 100 ml. Erlenmeyer flasks and autoclaved at 15 lb. pressure for 25 minutes. After autoclaving, the flasks were inoculated with equal amounts of inoculum from a seven-day old culture and incubated at 30° C.

The dry weight of the mycelium was recorded at the end of 21 days.

In order to find out the most suitable concentration of carbon and nitrogen for maximum growth and sporulation of the fungus,

different amounts of lactose, supplying 0–3% C and different levels of asparagine giving 0–2% N were incorporated in the basal medium.

The effect of carbon and nitrogen ratio was also investigated using different levels of carbon (lactose) and nitrogen (asparagine) in the medium. Four levels, each of nitrogen and carbon, were tried. These were normal, three-fourths, half and one-fourth normal.

Experimental Results

The results of the effect of several carbon sources and their concentrations on growth and sporulation of *C. capsici* are presented in Tables I and II.

Table I

Effect of several carbon sources on growth and sporulation of Colletotrichum capsici

	Carbohydrates	Weight of carbohydrates in grams per 100 ml.	Average dry weight of mycelium in mg.	Extent of sporulation	Final pH
1.	Lactose ..	2·999	255·6	Abundant	7·7
2.	Xylose ..	3·158	229·0	,,	8·0
3.	Sucrose ..	3·000	223·6	,,	8·2
4.	Glucose* ..	3·158	215·6	,,	8·3
5.	Dextrose* ..	3·158	204·0	,,	8·5
6.	Maltose ..	3·158	184·0	Near abundant	8·1
7.	Levulose ..	3·158	148·6	Abundant	8·0
8.	Mannitol ..	3·193	87·6	Trace	6·5
9.	Control ..	0·0	38·3	Nil	6·0

Critical difference at 1% level = 39·49; at 5% level = 28·66.

* Glucose and dextrose although synonymous were of different brands. Hence used to find out the effect of impurities, if any.

Although lactose recorded the highest mycelial output, it was not statistically different from that obtained with xylose. Sucrose, glucose, dextrose, maltose, levulose and mannitol were inferior to the above

two sugars in order. The control without any carbon source recorded the minimum mycelial growth. Abundant to near abundant sporulation was obtained on all carbohydrates except mannitol where it was scanty. In general, the pH shifted towards alkalinity with the various carbon sources except in the case of mannitol and the control where the respective media were acidic.

The effect of different carbon concentrations on the growth of *C. capsici* was next studied using lactose as the carbon source. The results are presented in Table II.

TABLE II

Effect of different concentrations of lactose on growth and sporulation of C. capsici

Treatments	Weight of lactose in grams per 100 ml.	Average dry weight of mycelium in mg.	Extent of sporulation	Final pH
No carbon ..	..	32·0	Nil	6·3
0·5% carbon ..	1·1876	107·0	Sparse	7·8
1·0% carbon ..	2·3752	184·3	Near abundant	7·9
1·263% carbon ..	2·9996	239·0	Abundant	7·7
1·5% carbon ..	3·5628	301·3	„	7·8
2·0% carbon ..	4·7504	366·3	„	7·0
2·5% carbon ..	5·9380	466·3	Very abundant	7·8
3·0% carbon ..	7·1256	427·3	Abundant	7·8

Critical difference at 1% level = 19·47; at 5% level = 14·03.

The growth of *C. capsici* increased with increasing concentrations of carbon up to 2·5%. The increase in mycelial output was about 94% over the basal standard medium containing 1·263% carbon, and was significantly superior to all other treatments. Sporulation was also very abundant at 2·5% carbon level.

The effect of different nitrogen sources, concentrations of nitrogen and different levels of carbon and nitrogen on growth and sporulation of the fungus was also investigated. The results are summarized in Tables III, IV, V *a* and V *b*.

TABLE III

Effect of different nitrogen sources on growth and sporulation of C. capsici

	Nitrogen sources	Weight of salts in grams per 100 ml.	Average dry weight of mycelium in mg.	Extent of sporulation	Final pH
1.	Asparagine ..	0·177	297·0	Abundant	5·1
2.	Peptone ..	0·206	279·0	Very abundant	5·1
3.	Urea ..	0·071	276·6	Moderate	5·2
4.	Potassium nitrate	0·238	258·3	Abundant	8·2
5.	Sodium nitrate	0·200	257·0	,,	8·3
6.	Calcium nitrate	0·221	218·6	,,	7·5
7.	Ammonium nitrate ..	0·094	203·6	Sparse	5·2
8.	Ammonium sulphate ..	0·155	109·0	Nil	2·6
9.	Control ..	..	97·0	Trace	4·4

Critical difference at 1% level = 42·38; at 5% level = 30·76.

1. Among the nitrogen compounds tested, asparagine proved to be the best source recording the maximum dry weight of mycelial output. This was followed in order by peptone, urea, potassium nitrate, sodium nitrate, calcium nitrate, ammonium nitrate and ammonium sulphate.

Statistically, there was no significant difference between the organic nitrogen compounds themselves (treatments 1, 2 and 3) although asparagine proved superior to all inorganic nitrogenous compounds. Asparagine, peptone and urea, as well as all the nitrates proved far superior to ammonium sulphate. The growth of the fungus was at a minimum in the control devoid of any nitrogen source.

2. For sporulation, peptone appeared to be the best followed by potassium nitrate, sodium nitrate, calcium nitrate and asparagine. Sporulation was moderate with urea and sparse in ammonium nitrate. Only traces of sporulation were observed in the control and none at all in the medium containing ammonium sulphate.

3. The pH of the medium containing potassium nitrate, sodium nitrate, or calcium nitrate shifted towards alkalinity, whereas ammonium sulphate lowered the pH markedly resulting in physiological acidity and eventual unsatisfactory growth. With peptone, asparagine, urea and ammonium nitrate, however, the original pH of the medium was maintained more or less.

TABLE IV

Effect of different concentrations of asparagine on growth and sporulation of C. capsici

Treatments	Weight of asparagine in grams per 100 ml.	Average dry weight of mycelium in mg.	Extent of sporulation	Final pH
0·0000% N ..	0·000	94·7	Sparse	4·5
0·0125% N ..	0·067	259·2	,,	4·5
0·025 % N ..	0·134	273·5	,,	4·8
0·033 % N ..	0·177	293·2	Abundant	5·1
0·050 % N ..	0·268	300·7	Trace	6·0
0·100 % N ..	0·536	307·0	Nil	6·3
0·150 % N ..	0·804	319·5	,,	6·8
0·200 % N ..	1·072	340·5	,,	7·6

Critical difference at 1% level = 17·16; at 5% level = 12·62.

The growth of *C. capsici* increased with an increase in the concentration of nitrogen. The maximum output was obtained with 0·02% nitrogen in the form of asparagine and this treatment was significantly superior to all other treatments, though satisfactory growth was obtained even at lower levels of nitrogen.

Sporulation was abundant only at 0·033% nitrogen level. In media containing 0·0125 and 0·025% nitrogen, sporulation was sparse. At levels higher than 0·033% nitrogen either no sporulation was evident or only traces were produced. On either side of 0·033% nitrogen level there was a change in the final pH of the medium.

From Tables V *a* and V *b*, the following conclusions could be drawn;

TABLE V *a*

Effect of carbon/nitrogen ratio on growth of C. capsici

Average mycelial growth of *C. capsici* in mg. at different C/N levels

Nitrogen / Carbon	1	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	Mean carbon
1	135·0	149·0	390·0	531·5	301·3
$\frac{3}{4}$	119·5	121·5	234·0	428·2	225·8
$\frac{1}{2}$	77·0	87·2	222·0	199·2	146·3
$\frac{1}{4}$	50·2	65·5	76·2	86·5	69·6
Mean nitrogen	95·4	105·8	230·5	311·3	..

Critical difference for N and C at 1% level = 9·86; at 5% level = 7·38. Critical difference for interaction (N × C) at 1% level = 19·71; at 5% level = 14·76.

TABLE V *b*

Effect of different C/N levels on sporulation of C. capsici

Nitrogen / Carbon	1	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$
1	Nil	Nil	Trace	Abundant
$\frac{3}{4}$	Nil	Nil	Trace	Abundant
$\frac{1}{2}$	Nil	Nil	Nil	Moderate
$\frac{1}{4}$	Nil	Nil	Trace	Moderate

1. Of all the levels tried, the medium containing carbon-nitrogen in the ratio of $1:\frac{1}{4}$ proved to be the best both for mycelial growth and sporulation.

2. At any level of nitrogen, a decrease in the carbon level resulted in a reduced yield. Conversely decreasing nitrogen levels increased the mycelial output at all carbon levels except at $\frac{1}{2}$ C: $\frac{1}{2}$ N level where the growth was slightly more than in the $\frac{1}{2}$ C: $\frac{1}{4}$ N ratio.

3. Moderate to abundant sporulation was produced at all levels of carbon when nitrogen was supplied at $\frac{1}{4}$th level. At other levels

of nitrogen either no sporulation was produced or only traces were observed.

4. The main effects of nitrogen and carbon as well as the interaction (N × C) were statistically highly significant.

Discussion

That in a study of the relationship between nutrition and growth, no one single factor determines the extent of growth but rather a complex of factors, all more or less interrelated, is well recognised. In the present investigations the carbon requirements for *Colletotrichum capsici* have been determined with sodium nitrate as nitrogen source and the nitrogen requirements with sucrose as the carbon source.

Of the various sugars tried (Table I) the maximum mycelial growth was observed on lactose and xylose and these were apparently the most readily available sources of carbon, when sodium nitrate was the sole source of nitrogen. Next in order were sucrose, glucose, dextrose, maltose and levulose. The alcohol mannitol was found to be poorly utilised. Thind and Randhawa (1957), however, reported that *C. capsici* grew best on dextrose, sucrose and maltose under their cultural conditions of investigation with potassium nitrate as the source of nitrogen.

Structural differences between sugars have been accounted for explaining differences in growth of fungi on various sugars (Cantino, 1949 *a*, *b*; Steinberg, 1942). This explanation apparently seems to hold good in the present study also.

Sporulation was abundant to near abundant on all sugars tried. Only traces were found on mannitol (Table I). Lactose, sucrose, glucose, levulose and xylose supported good sporulation. Thind and Randhawa (1957) observed that *C. capsici* sporulated best on pectin, maltose, starch and tartaric acid although sporulation was good on fructose, mannose, sucrose and melezitose also.

Increased concentrations of lactose increased the mycelial yield of *C. capsici* up to 2·5% carbon level beyond which growth decreased (Table II). Sporulation also increased with an increase in the concentration of carbon.

Studies on the nitrogen nutrition of *C. capsici* indicated that both organic and inorganic sources were fairly well utilized by the fungus except ammonium sulphate (Table III). But the organic source asparagine proved far superior to all inorganic nitrogenous compounds. Besides, peptone and urea as well as all nitrates were found to be superior to ammonium sulphate. Sporulation of the fungus was also suppressed in the presence of ammonium nitrogen. Thind and Randhawa (1957) obtained similar results with regard to ammonium sulphate.

It was observed that the increase in mycelial growth was proportional to the increase in the nitrogen concentration up to 0·2%N level (Table IV). Sporulation was, however, at a maximum with 0·033% N level and below or above this level, it was either sparse or nil. A C/N ratio of 1 : ¼ was best for growth and sporulation, when lactose and asparagine formed the carbon and nitrogen sources respectively. Growth decreased with decreasing carbon levels, nitrogen being held constant at ¼ level. Sporulation was also abundant to moderate with this ratio.

Summary

1. Of the carbohydrates tried lactose and xylose were most suitable for growth, at a carbon level of 2·5%. Next in order were sucrose, glucose and dextrose.

2. Among the nitrogenous compounds tested, asparagine proved to be one of the best sources, growth being most abundant at 0·2% N level. Peptone, urea, potassium and sodium nitrates also supported good growth of the fungus. But asparagine was found to be far superior to the inorganic nitrogen sources tried. Peptone supported maximum sporulation of the fungus.

3. A C/N ratio of 1 : ¼ was most suitable for maximum growth and sporulation.

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FUNGI FROM HYDERABAD (INDIA)—III

By P. N. Rao and M. A. Salam

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1. *Colletotrichum gomphrenae* Rao and Salam sp. nov. (Text-Fig. 2)

Infection spots hypophyllous, circular to semicircular with a pale ring enclosing a dull grey centre measuring 2–3 mm. in diameter. Acervuli amphigenous, dark and pointed. Setæ dark brown, 3–4 septate, straight and pointed, basal cell swollen into a knob, and are intermixed with conidiophores, measuring 36·0–136·8 × 3·6 μ. Conidiophores hyaline, straight and pointed. Conidia hyaline, 1-celled, cylindrical, straight, continuous, guttulate, with rounded or pointed ends, measuring 16·0–28·8 × 4·0–4·8 μ.

Habit.—On the living leaves of *Gomphrena decumbens* Jacq. (Amarantaceae), Osmania University Campus, 19–8–1958, P. N. Rao, O.U.B. Herb. 'Hy' No. 78.

***Colletotrichum gomphrenae* Rao and Salam sp. nov.**

Infectionis maculæ hypophyllae, circulares vel semicirculares. annulo pallido circum centrum obscurate griseum 2–3 mm. diam. Acervuli amphigeni, fuscu atque acuti. Setæ fusce brunneae, 3–4 septatae, rectae et acutae, cellula basali tumescente in nodum, intermixtae conidiophoris, magnit. 36·0–136·8 × 3·6 μ.

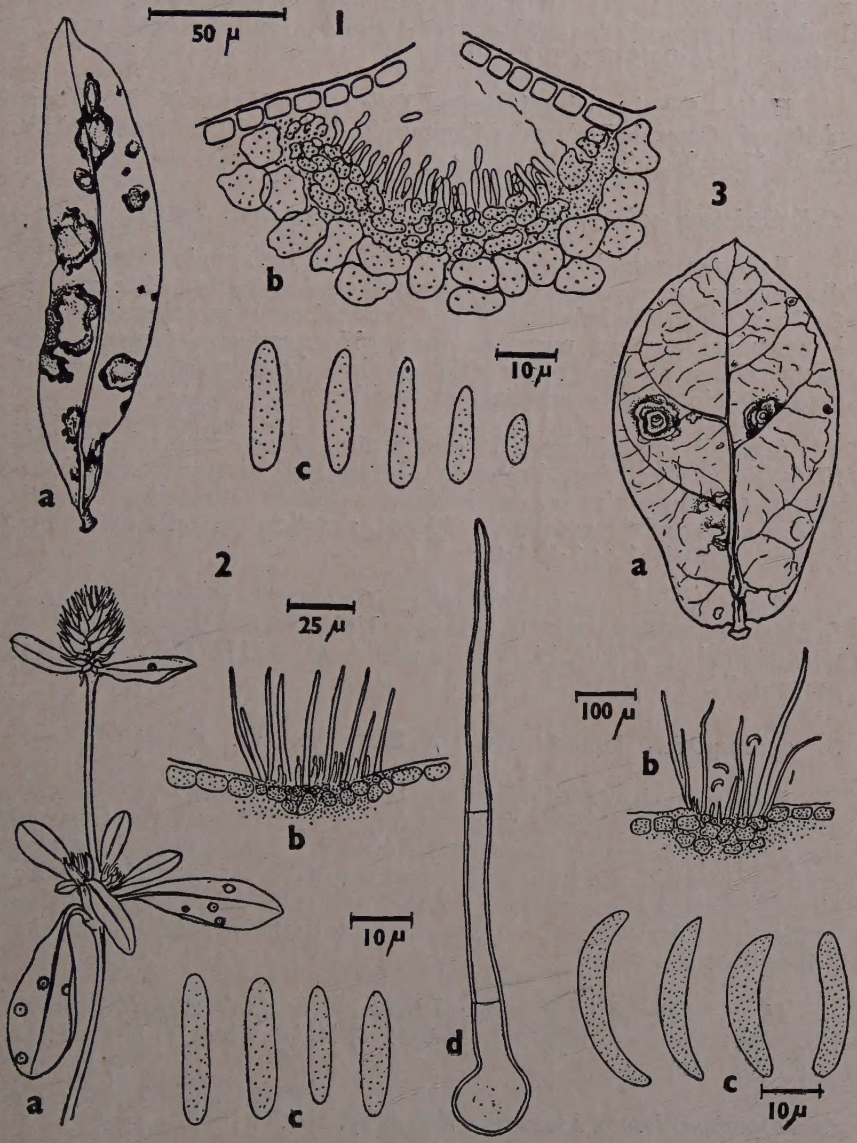
Conidiophori hyalini, recti et acuti. Conidia hyalina, semel cellulata, cylindrica, recta, continua, guttulata, apicibus rotundatis vel acutis, magnit. 16·0–28·8 × 4·0–4·8 μ.

Typus lectus in foliis viventibus *Gomphrenae decumbentis* Jacq. e familia Amaran-tacearum in Campo Universitatis Osmania, die 19 augusti anni 1958 a P. N. Rao et positus in O.U.B. Herb. 'Hy' sub numero 78.

2. *Colletotrichum calotropidis* Rao and Salam sp. nov. (Text-Fig. 3)

Leaf spots epiphyllous, circular in dark concentric rings, purplish when young becoming greyish white, measuring 5–12 mm. in diameter. In the case of severe infection, 2–3 spots coalesce to form a big purplish patch. Sometimes a shot-hole effect is noticeable. Leaves with severe infection slowly curl up, becomes chlorotic, wither and fall off.

Acervuli sub-epidermal, erumpent, dark brown, measuring 57·6–96·0 μ. Setae dark brown, 3–4 septate, pointed, straight, intermixed



TEXT-FIGS. 1–4.—Fig. 1. *Gloeosporium loranthi*: (*a*) Infected leaf showing typical symptoms. (*b*) Acervulus with conidiophores and conidia. Fig. 2. *Colletotrichum gomphrenae*: (*a*) Plant showing infected leaves. (*b*) Acervulus. (*c*) Conidia. (*d*) Seta. Fig. 3. *Colletotrichum calotropidis*: (*a*) Infected leaf with concentric spots. (*b*) Acervulus. (*c*) Conidia.

with a small hyaline palisadely arranged conidiophores. Conidia hyaline, single-celled, sickle-shaped, simple, guttules not present, measuring 16·0–19·8 × 3·2–4·0 μ.

Habit.—On the living leaves of *Calotropis gigantea* R. Br. (Asclepiadaceæ), Osmania University Campus, 22–8–1958, P. N. Rao, O.U.B. Herb. 'Hy' No. 79.

***Colletotrichum calotropidis* Rao and Salam sp. nov.**

Foliorum maculæ epiphyllae, circulares in annulo concentricos dispositae, purpurascentes in statu juvenili, evadentes griseoalbae, magnit. 5–12 mm. diam. In infectione severa binæ vel ternæ maculae coalescunt in maculam amplam purpurascentem. Nonnumquam foramen tamquam bellicae glandis notatur. Folia serio infecta paulatim crispantur, evadunt chlorotica, evanescunt et decidunt.

Acervuli subepidermales, erumpentes, fusce brunnei, magnit. 57·6–96·0 μ. Setae fusce brunneae, 3–4 septatae, acutae, rectae, intermixtæ conidiophoris parvis hyalinis vallatum dispositis. Conidia hyalina, una cellula constantia, falcata, simplicia, guttulis absentibus, magnit. 16·0–19·8 × 3·2–4·0 μ.

Typus lectus in foliis viventibus *Calotropidis giganteae* R. Br. e familia Asclepidacearum in Campo Universitatis Osmania die 22 augusti anni 1958 a P. N. Rao et positus in O.U.B. Herb. 'Hy' sub numero 79.

3. ***Gloeosporium loranthi* Rao and Salam sp. nov.** (Text-Fig. 1)

Leaf spots hypophyllous, dark brown or purplish, with a white centre, circular, later becoming rounded or squarish or even elongated, measuring 3–12 mm. in diameter. Acervuli subepidermal, erumpent, conic or discoid, dark brown measuring 90·0–144·0 × 54·0–79·3 μ. Conidiophores hyaline, simple, arranged in a palisade manner. Conidia hyaline, 1-celled, smooth ellipsoidal with rounded ends, measuring 8·0–16·0 × 3·2–4·0 μ.

Habit.—On the living leaves of *Dendrophthoe falcata* (L.f.) Ettingsh. (Loranthaceae), Secunderabad, 5–8–1958, P. N. Rao, O.U.B. Herb. 'Hy' No. 80.

***Gloeosporium loranthi* Rao and Salam sp. nov.**

Maculae foliorum hypophyllae, fusce brunneae vel purpurascentes, centro albido, circulares, postea evadentes rotundatae vel plus minusve quadratae vel etium elongatae, magnit. 3–12 mm. diam. Acervuli subepidermales, erumpentes, conici vel discoidei, fusce brunnei, magnit. 90·0–144·0 × 54·0–79·3 μ. Conidiophori hyalini, simplices, dispositi vallatim. Conidia hyalina una cellula constantia, lævia, ellipsoidea apicibus rotundatis, magnit. 8·0–16·0 × 3·2–4·0 μ.

Typus lectus in foliis viventibus Dendrophoes falcatae Ettingsh e familia Loranthacearum ad Secunderabad, die 5 augusti anni 1958 a P. N. Rao et positus in O.U.B. Herb. 'Hy' sub numero 80.

SUMMARY

In this paper three new species of Melanconiales collected from Hyderabad are described. Duplicate sets of herbarium of new species are deposited in the Herb. Crypt. Ind. Orient of the Agricultural Research Institute, New Delhi.

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